

THE CRANIAL ANATOMY AND  
RELATIONSHIPS OF THE SYNAPSID *VARANOSAURUS*  
(EUELYCOSAURIA: OPHIACODONTIDAE) FROM THE  
EARLY PERMIAN OF TEXAS AND OKLAHOMA

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ABSTRACT

The cranial anatomy of the Early Permian synapsid *Varanosaurus* is restudied on the basis of previously described specimens from Texas, most importantly the holotype of the type species *V. acutirostris*, and a recently discovered, excellently preserved specimen from Oklahoma. Cladistic analysis of the Eupelycosauria, using a data matrix of 95 characters, provides the following hypothesis of relationships of *Varanosaurus*: 1) *Varanosaurus* is a member of the family Ophiacodontidae; 2) of the ophiacodontid genera included in the analysis, *Varanosaurus* and *Ophiacodon* share a more recent common ancestor than either does with the more primitive *Archaeothyris*; and 3) a clade containing the progressively more derived taxa Edaphosauridae, *Haptodus*, and Sphenacodontoidae (Sphenacodontidae plus Therapsida), together with Varanopseidae and Caseasauria, are progressively more distant outgroups or sister taxa to Ophiacodontidae. A revised diagnosis is given for *Varanosaurus*.

INTRODUCTION

Published accounts of the Early Permian synapsid *Varanosaurus* have been limited almost entirely to rather brief descriptions based on a few poorly preserved and/or incomplete skeletons collected from the Lower Permian of north-central Texas. The holotype of the type species *Varanosaurus acutirostris* was described originally by Broili (1904) and consists of an incomplete articulated skeleton (BSPHM 1901 XV 20), including most importantly the greater portion of the skull, collected from the Arroyo Formation, Clear Fork Group. With further preparation of the holotype, additional descriptions were provided by Broili (1914) and Watson (1914). A second specimen of *V. acutirostris*, collected from the same beds as the holotype and consisting of the greater portion of an articulated skeleton (AMNH 4174) that includes a fragment of the skull, was described by Case (1910) as *Poecilospondylus francisi*. Romer and Price (1940) later recognized *P. francisi* as a junior synonym of *V. acutirostris*, noting that they differ only in the former being about 20% larger in linear dimensions. A second species, *V. wichitaensis*, based originally on only a pelvis (MCZ 1353) from the Belle Plains Formation

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(Petrolia Formation of Hentz, 1988), Wichita Group, was described very briefly by Romer (1937). Additional isolated postcranial elements from the same beds as the holotype were referred to *V. wichitaensis* by Romer and Price (1940), who distinguished it from the type species by its somewhat smaller size and earlier occurrence. We suspect, however, that restudy of *V. wichitaensis* may require synonymizing it with the type species (Reisz, 1986). A detailed description of the axial skeleton of *V. acutirostris* by Sumida (1989) has been the only restudy of the anatomy of this animal since the monographic "Review of the Pelycosauria" by Romer and Price (1940).

The focus of this study is the cranial anatomy of *Varanosaurus*, which in previous studies was based almost exclusively on the holotype of *V. acutirostris*. Although Broili (1904, 1914) and Watson (1914) described the skull in some detail, Romer and Price (1940) attempted the only restoration, largely using the earlier studies with some information provided by a newly discovered snout (FMNH UC 34) from the Arroyo Formation and the "*Poecilospondylus*" specimen (AMNH 4174). Despite these descriptions there are large gaps in our understanding of the cranial anatomy of *Varanosaurus*. The availability of a nearly complete skull with an associated atlas-axis complex (FMNH PR 1760) collected by one of us (JRB) from the Lower Permian, Arroyo-equivalent beds in central Oklahoma has provided much of the impetus for this study, as has extensive preparation of the holotype of *Varanosaurus acutirostris*. We refer the Oklahoma specimen to *V. acutirostris*.

The following acronyms are used to refer to the institutional repositories of specimens: AMNH, American Museum of Natural History, New York; BSPHM, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; FMNH, Field Museum of Natural History, Chicago.

Key to abbreviations used in figures for anatomical structures: a, angular; ar, articular; ati, atlantal intercentrum; atn, atlantal neural arch; atr, atlantal rib; as, astragalus; ax, axis; axi, axial intercentrum; axr, axial rib; bo, basioccipital; ca, calcaneum; co, coronoid; cp, cultriform process; d, dentary; e, ectopterygoid; ept, epipterygoid; ex, exoccipital; f, frontal; h, hyoid; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pa, proatlas; pal, palatine; pf, postfrontal; ph, phalanges; pm, premaxilla; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; r3, third rib; s, stapes; sa, surangular; sm, septomaxilla; so, supraoccipital; sp, splenial; sph, sphenethmoid; sq, squamosal; st, supratemporal; t, tabular; ta, tarsus; v, vomer.

#### SYSTEMATIC PALEONTOLOGY

Order Synapsida Osborn 1903

Suborder Eupelycosauria Kemp 1982

Family Ophiacodontidae Nopsca 1923

Genus *Varanosaurus* Broili 1904

*Synonym.*—*Poecilospondylus* Case 1910.

*Type Species.*—*Varanosaurus acutirostris* Broili 1904.

*Revised Diagnosis.*—Ophiacodontid synapsid distinguishable from other members of the family by the following autapomorphic features: step-like lateral expansion of ventral margin of the anterior end of the maxilla in which the first 13 or 14 marginal teeth are implanted, with a marked increase in the posterior end



of the expansion that encloses the canines; lateral and dorsal surfaces of snout flat and separated by sharp ridge; dorsal process of premaxilla bifurcated; lateral surface of septomaxilla small with partial facial exposure; lacrimal narrowly contacts external naris; posterior process of jugal dorsoventrally narrow; middorsal margin of the quadratojugal forms the lateral wall of a narrow, shallow, trough-like channel that is bounded medially by the jugal and opens dorsally; as many as 56 marginal maxillary teeth; bases of maxillary teeth, particularly the caniniform and large midseries teeth, slightly compressed anteroposteriorly, giving them an oval outline in cross section; caniniform teeth equal to or greater than twice the length of the longest maxillary teeth; tabular does not extend ventrally to level of ventral margin of supraoccipital and does not contact the opisthotic, so that the posttemporal fenestra is open laterally; short, posteromedially-directed flange of the quadrate ramus of the pterygoid, the postbasal process, forms the posterior wall of a deep socket into which the basiptyergoid process of the braincase fits; cultriform process of parasphenoid extremely long, narrow, and low, and extends anteriorly to approximately the level of the posterior border of the internal naris; narrow margin along the dorsal border of the medial ascending lamina of anterior ramus of pterygoid supports cultriform process of parasphenoid for nearly its entire length; mandibular symphysis formed only by dentary; dorsal process of stapes projects at nearly a right angle from the shaft, and its distal end contacts the anteroventral (internal) surface of the tabular; swollen neural arches; alternation of neural spine height of presacral vertebrae.

*Varanosaurus acutirostris* Broili 1904, p. 71

*Synonym.* — *Poecilospondylus francisi* Case 1910, p. 183.

*Diagnosis.* — As for genus.

*Holotype.* — BSPHM 1901 XV 20, an incomplete articulated skeleton that includes greater part of skull.

*Horizon and Locality.* — Arroyo Formation, Clear Fork Group, Lower Permian of the Craddock Bonebed, Craddock Ranch, north of Seymour, Baylor County, Texas.

*Referred Specimens.* — AMNH 4174, holotype of *Poecilospondylus francisi*, greater portion of articulated skeleton that includes a fragment of the skull from the Arroyo Formation, Clear Fork Group, Lower Permian of Coffee Creek, Baylor County, Texas; FMNH UR 34, portion of snout from same horizon and locality as that for AMNH 4174; FMNH PR 1760, nearly complete skull with atlas-axis complex attached from the Wellington Formation (Lower Permian), SW $\frac{1}{4}$  sec. 19, T3N, R1E, Garvin County, Oklahoma (South Pauls Valley Locality of Olson, 1967).

#### DESCRIPTION

*General.* — The reconstruction of the skull of *Varanosaurus* shown in Fig. 1–3 is based on the nearly complete, well-preserved skulls BSPHM 1901 XV 20 (Fig. 4–9) and FMNH PR 1760 (Fig. 10–15). Being able to cross check between the two skulls has greatly enhanced the accuracy of the reconstruction. Study of their palates, however, is greatly hindered by the closely attached mandibles. This problem was partially resolved through the use of CAT (computerized axial tomography) scans of BSPHM 1901 XV 20. The partial snout of FMNH UR 34 has been particularly important in interpreting the structure of the internal naris and the anterior end of the palate. The posterior portion of the lower jaw is preserved only in FMNH PR 1760. It has been possible to reconstruct the entire

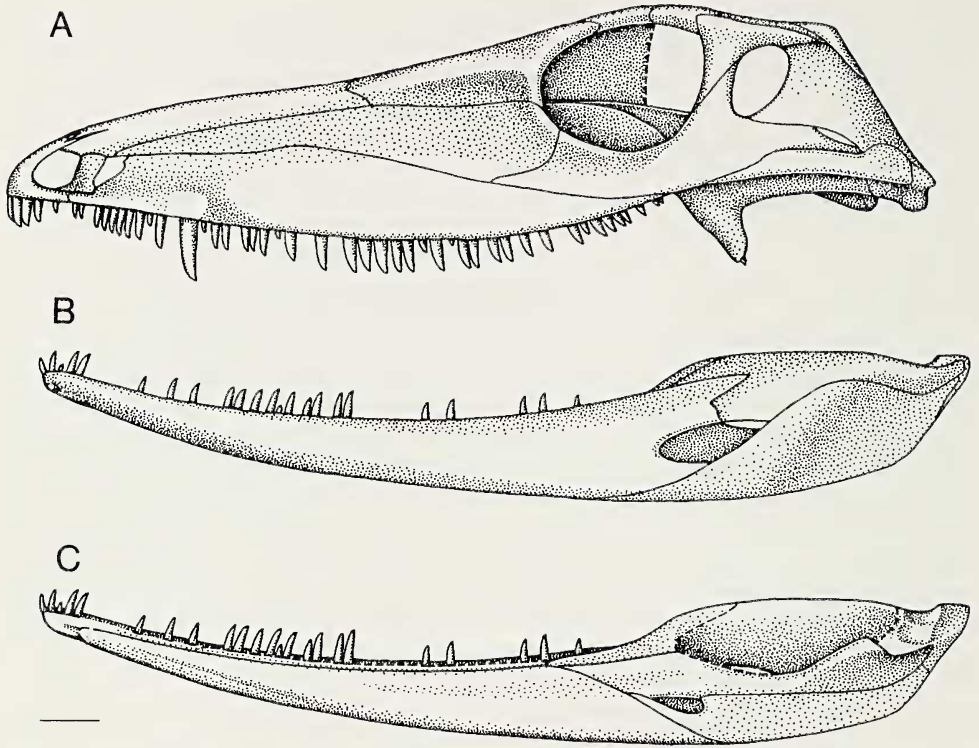


Fig. 1.—Reconstruction of *Varanosaurus acutirostris*. A, skull in lateral view; lower jaw in B, lateral, and C, medial views. Scale = 1 cm.

lateral surface of the lower jaw and all but the region of the adductor fossa of the medial surface.

The skull is long, low, and narrow. The antorbital region is particularly long, with the distance from the level of the anterior border of the orbit to the tip of the snout measuring about two and one-fourth times as long as the distance from the level of the posterior border of the orbit to the posteroventral corner of the skull. In lateral view the dorsal margin of the skull is slightly concave between the levels of the posterior margin of the external naris and the midlength of the orbit. More posteriorly it slopes gradually ventrally to the occipital margin. The ventral margin of the skull is slightly convex from the tip of the snout to the level of the postorbital bar, with the remaining posterior portion curving slightly ventrally. The external naris is divided into two openings by the septomaxilla. A larger anterior orifice, undoubtedly the true external naris, is subcircular in outline, whereas the posterior orifice, whose function is uncertain, has roughly the outline of a right triangle, with the hypotenuse forming the posteroventral margin. The posterior orifice is undoubtedly an expansion of the septomaxillary foramen seen in some pelycosaurs (Romer and Price, 1940) and therapsids (Wible et al., 1990). The orbit appears subcircular in lateral view, with some flattening of the dorsal rim. The flattening is due to the fact that most of the dorsal half of the orbit extends into the nearly horizontal skull table and therefore faces dorsally. As is typical of synapsids, a lateral temporal fenestra is located directly behind the orbit

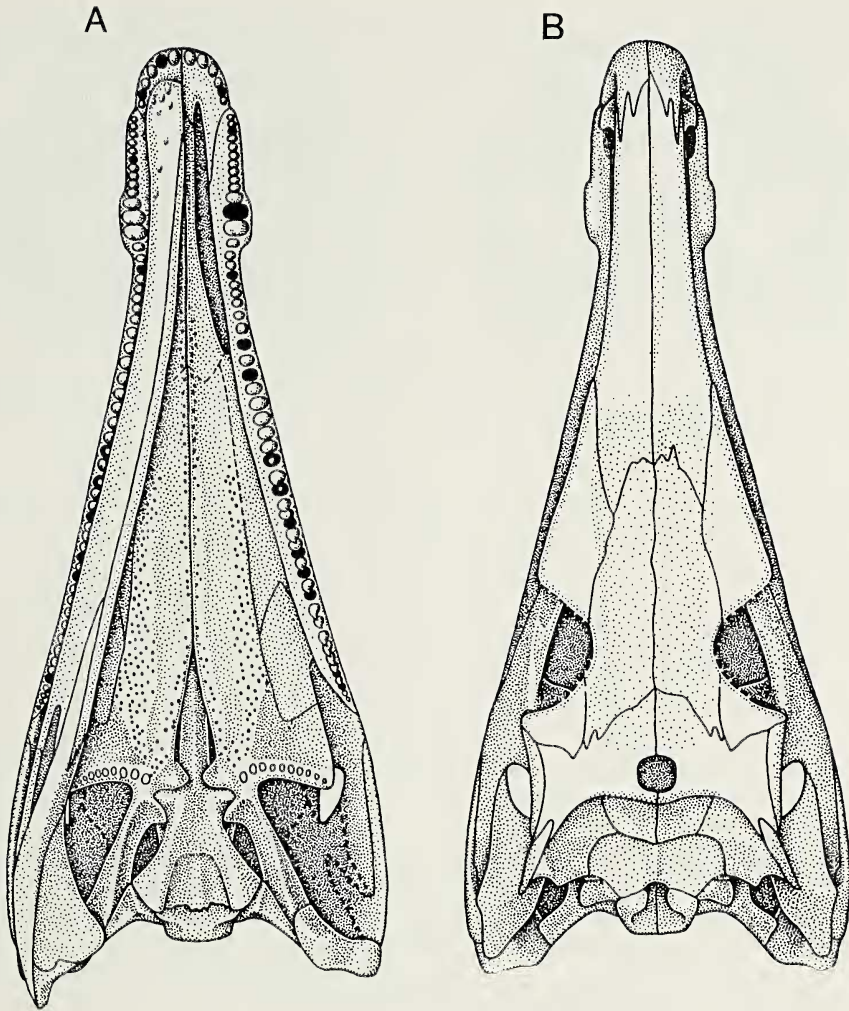


Fig. 2.—Reconstruction of the skull of *Varanosaurus acutirostris* in A, ventral (palatal), and B, dorsal views. Right lower jaw attached in A. Scale = 1 cm.

and is bordered by the postorbital, squamosal, and jugal. The opening, which is relatively small compared to those of most other synapsids, has the outline of a right triangle with rounded corners, and with the hypotenuse being posteroventral. On both sides of the skull of FMNH PR 1760 there is a small, very narrow, elliptical opening posteroventral to the true temporal fenestra and along the squamosal-jugal suture. A similar opening occurs occasionally in *Ophiacodon* (Romer and Price, 1940).

In dorsal view the outline of the skull is narrowly triangular, tapering steadily anteriorly from its widest point at the level of the occiput to its narrowest point at about midlength of the nasal bone. At this point there is an abrupt expansion of the snout due to a shelf-like, lateral expansion of the ventral margin of the maxilla. More anteriorly the snout narrows very slightly to its bluntly rounded



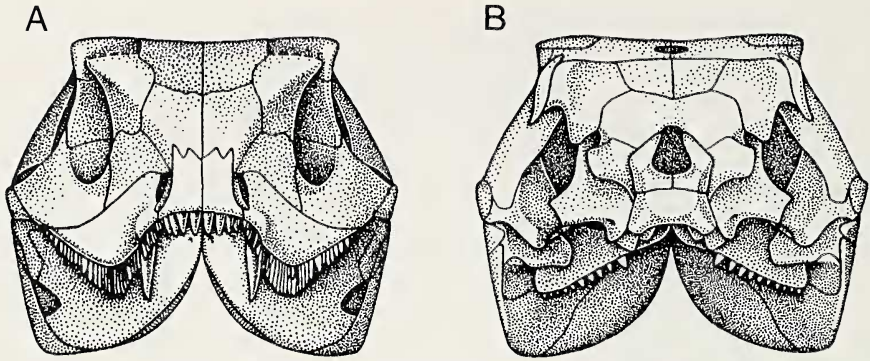


Fig. 3.—Reconstruction of the skull of *Varanosaurus acutirostris* with lower jaws attached in A, anterior, and B, posterior (occipital) views. Scale = 1 cm.

tip. The dorsal skull table is nearly flat in transverse section from the occipital margin to within a very short distance of the snout tip. Anterior to the orbits the dorsal table and lateral cheek regions of the skull meet in a thickened, right-angled corner that becomes more pronounced posteriorly as it forms a slightly laterally jutting ridge. The ridge meets a low, ridge-like thickening of the orbital margin to produce a shallow, preorbital depression or pocket that includes the ventral, laterally facing portion of the prefrontal and the adjoining margin of the lacrimal. The orbits appear as sharply and deeply incised, semicircular notches in the lateral margins of the skull table. Antorbitally the skull table narrows quickly to about midlength of the nasals, then continues little changed. The ventral posterolateral corners of the skull extend only a short distance beyond the level of the occipital condyle.

The lateral margins of the palate are obscured by the attached lower jaws in BSPHM 1901 XV 20 and FMNH PR 1760, but far less so in the latter. Some of the palatal sutures in FMNH PR 1760 remain obscured by a thin veneer of matrix that could not be removed without loss of the shagreen of teeth that cover much of the palate. The internal nares are very narrow, but greatly elongated antero-posteriorly, with a width-to-length ratio of about 0.06.

The occipital surface of the skull is moderately concave and inclined strongly anterodorsally at approximately 45°. In both BSPHM 1901 XV 20 and FMNH PR 1760 the region of the foramen magnum is partially obscured by the attached atlas-axis complex.

The lower jaw is very shallow in lateral view. The tooth-bearing margin is only very slightly concave, and the coronoid eminence is very low, rising only slightly above the level of the jaw joint facet of the articular. The ventral margin of the jaw forms an essentially unbroken, very slightly convex curve except for a marked upturn a short distance from its posterior end. A horizontally elongate oval mandibular foramen opens on the lateral surface of the jaw at the intersection of the dentary, angular, and surangular. A much smaller opening, the Meckelian fenestra, is present on the medial surface of the jaw on the angular-prearticular suture a short distance behind its intersection with the posterior margin of the splenial.

*Skull Roof.*—The small, lightly built premaxilla possesses, or has spaces for, six teeth. Its narrow maxillary process, forming the ventral border of the anterior orifice of the external naris, has a long, overlapping contact with the medial surface of the premaxillary process of the maxilla. The dorsal surface of the premaxilla

is extremely long and narrow, and its basal portion borders the anterior dorsal half of the anterior narial orifice. The distal portion, which is complete only in BSPHM 1901 XV 20, divides into two splinter-like processes, the lateral one being longer, that overlap the nasal for a considerable distance.

Although none of the specimens has a complete premaxillary dentition, the size relationships of the teeth can be determined. The first three teeth are the largest of the series and are subequal in size, the fourth and fifth are subequal in size and noticeably smaller, and the sixth is smaller still. For the greater part of their basal length the teeth are slightly compressed mediolaterally and have a rather constant narrow diameter, giving them an elongate, somewhat columnar appearance. The tips are sharply pointed and curved weakly posteromedially. Although the premaxillary teeth are too poorly preserved to determine the presence of fore and aft cutting edges, these are demonstrable in the few well-preserved maxillary and dentary teeth.

The septomaxillae are well preserved and in their proper position in BSPHM 1901 XV 20; only the right is present in FMNH PR 1760, but it is incompletely developed and has been displaced so as to be exposed on the ventral margin of the naris with its medial surface facing laterally and its vertical axis horizontal. The septomaxilla is basically a vertical, triangular sheet of bone that extends anteromedially. Its base rests on the premaxillary-maxillary suture laterally, but solely on the premaxilla medially, as it extends to nearly the midline of the skull. The medial expansion of the septomaxilla is probably homologous with the medial transverse shelf identified in pelycosaurs and therapsids and believed to have formed a partial roof for the anterior portion of Jacobson's organ (Romer and Price, 1940; Wible et al., 1990). The dorsal apex or process of the septomaxilla overlaps slightly the ventral lateral margin of the nasal and is narrowly separated from the lacrimal. The external edge or surface of the septomaxilla is narrow, slightly concave, and unsculptured near its ventral end, whereas dorsally it gradually widens and its sculptured surface presumably indicates a facial exposure. The anterolateral surface of the septomaxilla is concave due to a lip-like expansion of its base. Just above and near the lateral end of the expanded base the bone is pierced by a short, anteroposterior canal, the septomaxillary canal, which Wible et al. (1990) believed carried branches of the superior labial nerve and artery. The posterior orifice of the external naris, identified as the septomaxillary foramen, is enlarged in *Varanosaurus* compared to other Permo-Carboniferous synapsids. Several functions have been attributed to this opening, the most recent interpretation being that the infraorbital nerve and artery may have passed through it (Wible et al., 1990).

The nasal is relatively long, forming slightly over 50% of the midline length of the skull roof and having a length approximately 60% longer than that of the frontal. The greater portion of the nasal is exposed on the skull table, but a narrow, lateral portion is directed in an abrupt right angle ventrally onto the cheek region. The nasals diminish little in width anteriorly, where they end by not only having a deeply penetrating exposure between the dorsal processes of the premaxillae, but also extending along their lateral margin to form the posterodorsal and anterodorsal borders of the true external naris and the septomaxillary foramen, respectively. The frontals are exposed entirely on the skull table. They are basically subrectangular, the main exceptions being a broad encroachment at their posterior midline union by the paired parietals and a minor incisement of their lateral margins by the orbit. From its contribution to the orbit the anterior extension or process of the frontal is roughly three times that of the posterior extension or



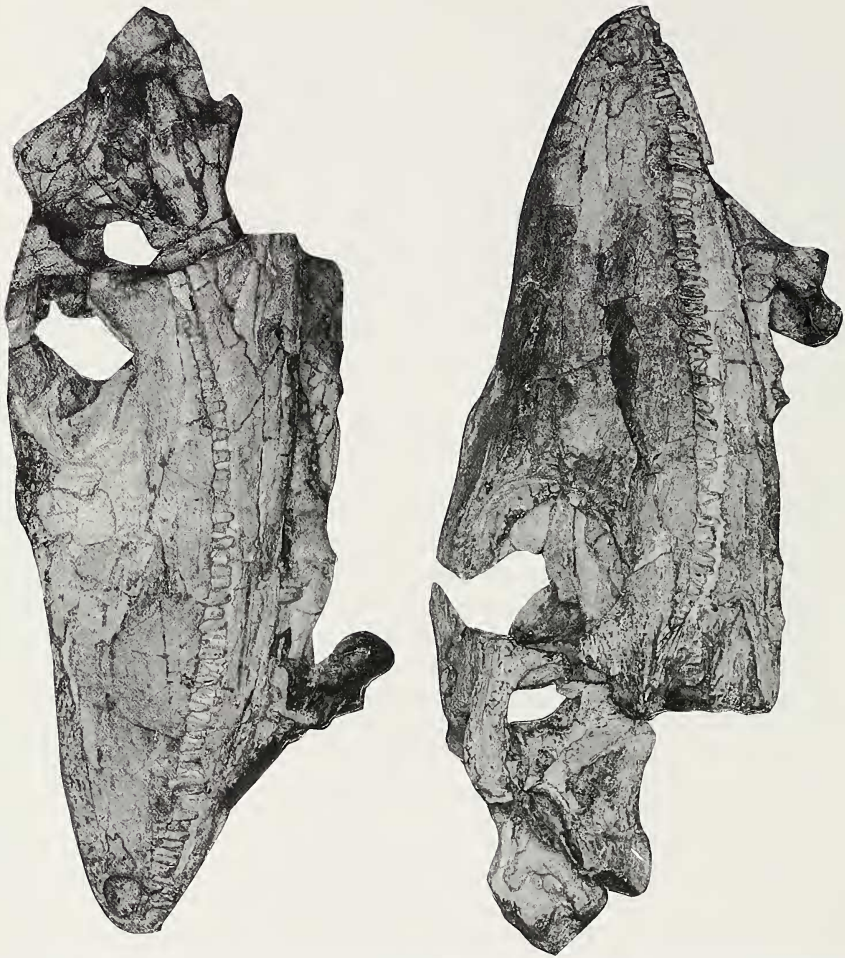


Fig. 4.—*Varanosaurus acutirostris*, holotype, BSPHM 190 XV 20. Lateral views of skull with attached partial lower jaws. Scale as in Fig. 5.

process. The parietal is short, having a midline length equal to its transverse width, and nearly reaches the lateral margin of the skull table. The occipital margin is slightly concave, with the posterolateral corner of the bone being drawn out into a narrow, wing-like process that underlies approximately the anterior half of the supratemporal. An extremely narrow exposure of the lateral margin of the posterolateral wing of the parietal extends between the supratemporal and post-orbital to contact the squamosal. The pineal foramen is large and positioned near the occipital border; the lip of its margin is not raised. The paired postparietals form a roughly trapezoidal plate which is restricted to the occiput.

The prefrontal forms the entire anterodorsal margin of the orbit as a thickened, rounded rim. The ventral end of its orbital margin continues for a short distance as a narrow, ventral process along the anterior wall of the orbit and medial to the external orbital margin of the lacrimal. An abrupt right angle bend sharply divides the prefrontal longitudinally into a dorsal table and a lateral cheek exposure. Its



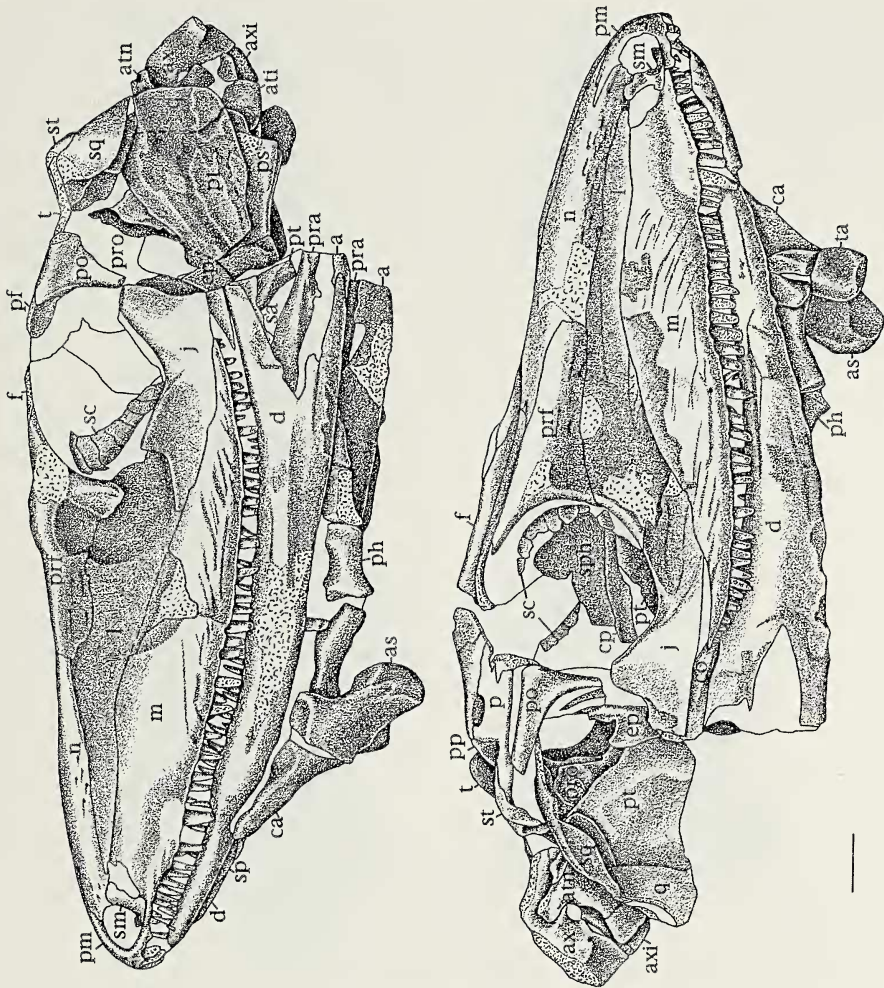


Fig. 5.—Illustrations of *Varanosaurus acutirostris*, holotype, BSPHM 190 XV 20 as seen in Fig. 4. Scale = 1 cm.

dorsal table component contacts the lateral margin of the frontal, then tapers laterally for most of its remaining anterior length as it extends between the nasal and lacrimal. Anteriorly the prefrontal ends in a short, nearly vertical contact with the nasal on the lateral surface of the skull. External exposure of the postfrontal is restricted to the skull table and has roughly the outline of an equilateral triangle. Its entire anterolateral margin forms the posterodorsal rim of the orbit, whereas its straight medial margin contacts the frontal except for possibly a small contact with the parietal at its posterior end. Nearly the entire posterior margin of the postfrontal contacts the parietal, ending medially in a posteriorly-directed, spike-like projection. The extreme lateral end of the posterior margin of the postfrontal contacts the postorbital. The postfrontal extends a short distance posteroventrally from the anterior margin of its contribution to the posterodorsal orbital rim to form the dorsal end of a transversely broad, posterior wall of the



Fig. 6.—*Varanosaurus acutirostris*, holotype, BSPHM 190 XV 20. A, dorsal, and B, ventral (palatal) views of skull with attached partial lower jaws. Scale as in Fig. 7.

orbit. The postorbital is roughly triradiate in lateral view, forming the dorsal half of the posterior orbital rim and most of the dorsal margin of the temporal fenestra. The short, stout anterodorsal process contacts the postfrontal, the ventral post-orbital process has a long anteroventrally oblique contact with the jugal, and the distal end of the posterior process has a broad contact with the squamosal. The posterior process, which has a very narrow exposure along the lateral margin of the skull table, is separated narrowly from the supratemporal by the parietal. A narrow flange projects medially from the internal surface of the ventral process just posterior to the orbital margin to form the central portion of a posterior orbital wall.

In keeping with the general profile of the skull the maxilla is very low, with a height equal to about 15% of its length. The ventral margin is slightly convex, and the dorsal lamina reaches a greatest height a short distance anterior to its



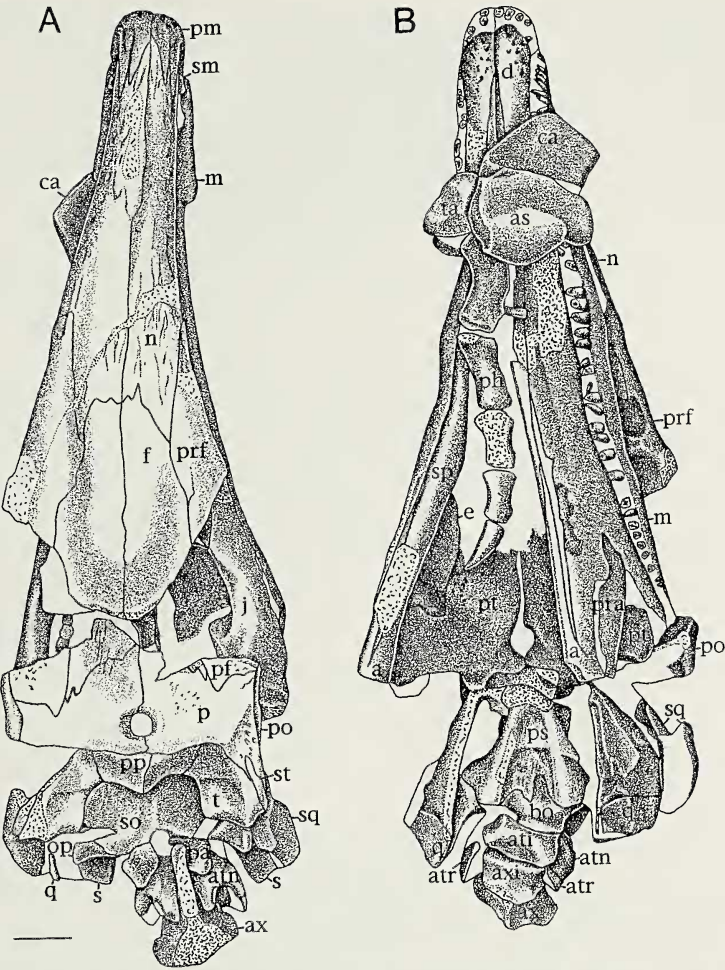


Fig. 7.—Illustrations of *Varanosaurus acutirostris*, holotype, BSPHM 190 XV 20 as seen in Fig. 6. Scale = 1 cm.

midlength and well posterior to the level of the caniniform tooth pair. The maxilla terminates anteriorly in the formation of the posterior border of the septomaxillary foramen, and in the premaxillary process that extends below the septomaxilla but does not reach the true external naris. The maxilla has approximately 55 teeth and tooth spaces. The ventral margin of the lateral surface of the anterior end of the maxilla exhibits a step-like expansion in which the first 14 teeth, ending with the noticeably larger or caniniform tooth pair, are implanted. For most of its length the lateral expansion of the maxilla is weakly developed and is pronounced only at its posterior end, where it accommodates the caniniform tooth pair. The precaniniform teeth exhibit a steady decrease in size anteriorly. The anterior eight postcaniniform teeth are slightly smaller than the last precaniniform tooth, followed by about eight teeth of subequal size that are slightly larger than the last precaniniform tooth, and the remainder of the series decreases gradually posteriorly. Tooth morphology is like that of the premaxillary teeth. For much of their





Fig. 8.—*Varanosaurus acutirostris*, holotype, BSPHM 190 XV 20. Skull in posterior (occipital) view. Scale as in Fig. 9.

basal length they are rather slender with a nearly constant diameter and slightly compressed anteroposteriorly, giving them a somewhat columnar appearance. The sharply pointed tips of the teeth are weakly curved posteriorly. The absence of portions of the left dentary, lacrimal, and nasal of the snout fragment of FMNH UC 34 allows some description of the supracanine buttress on the medial surface of the maxilla. The supracanine buttress is well developed as a medially and dorsally rounded swelling of the alveolar shelf that extends between the levels of the caniniform tooth pair and about the fourth or fifth precanine tooth. The buttress increases in size posteriorly, and the posterior end of its dorsal surface extends dorsally as a narrow, vertical ridge, referred to as the dorsal ascending process, on the medial surface of the dorsal lamina of the maxilla. The ascending process is broadly rounded in horizontal section and thus is not set off sharply from the medial surface of the maxilla; it appears not to reach the dorsal margin of the maxilla.

The lacrimal is exceptionally long and narrow. From its small contribution to the orbit it expands immediately for a short distance anteriorly, then gradually narrows as it extends to its very small contribution to the posterior dorsal margin of the expanded septomaxillary foramen. The lacrimal exhibits a pronounced, step-like thickening near the orbital margin of its medial surface. The thickening, which is partially exposed in medial view of the right lacrimal in FMNH PR 1760 (Fig. 10, 11), has the outline of a crescent with the ends rounded and the concave margin directed anteriorly; matrix obscures the medial surface of the lacrimal anterior to the orbital thickening. The dorsal half of the crescent-shaped thickening is continuous posteriorly with the ventral orbital process of the prefrontal that extends along the anterior wall of the orbit and medial to the orbital margin of

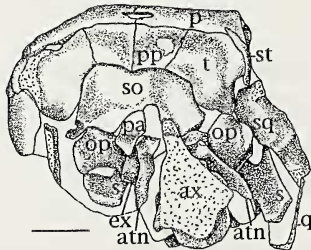


Fig. 9.—Illustration of *Varanosaurus acutirostris*, holotype, BSPHM 190 XV 20 as seen in Fig. 8. Scale = 1 cm.

the lacrimal. The posteroventral margin of the ventral half of the medial thickening of the lacrimal (not visible in Fig. 10, 11) undoubtedly corresponds in position to the lacrimal–jugal contact. In FMNH PR 1760 matrix obscures the medial surface of the right lacrimal anterior to its orbital thickening.

The triradiate jugal has an extensive lateral exposure. A wide suborbital process forms the entire ventral orbital margin, then quickly tapers ventrally to form a short, spike-like anteroventral projection. The suborbital process narrowly enters the ventral margin of the skull, preventing a maxillary–quadratojugal contact. The postorbital process reaches only a short distance dorsally between the orbit and temporal fenestra, forming approximately the ventral half of the postorbital bar and ending in a posterodorsally oblique suture with the postorbital. A long, narrow posterior process of the jugal extends posteriorly beyond the ventral margin of the temporal fenestra and between the squamosal and quadratojugal. It tapers posteroventrally to a sharp point, and forms the ventral margin of the small, narrow, secondary lower temporal opening bordered dorsally by the squamosal. A medial flange recessed slightly from just below the level of the orbital rim at the base of the postorbital process of the jugal forms a large ventral portion of the posterior wall of the orbit. The medial orbital flange, best seen in FMNH PR 1760 (Fig. 12A, 13A), is continuous posterodorsally with that of the postorbital. A narrow notch separates the lateral edge of the anterior end of the medial orbital flange from the medial surface of the jugal proper.

The quadratojugals are present only in FMNH PR 1760, where they are well preserved. The quadratojugal has the general form of a slender horizontal band that extends for its entire length along the ventral margin of the skull. The dorsal margin of its posterior end has a semicircular expansion that overlaps the squamosal and quadrate, whereas anteriorly it tapers ventrally to a sharply pointed, wedge-shaped process. The central portion of the quadratojugal bows outward slightly so as to diverge dorsally slightly from the dorsomedially sloping plane of the cheek. As a result, the quadratojugal forms the lateral wall of a narrow, shallow, trough-like channel that opens dorsally and is bounded medially by the jugal. The lateral lip of the channel is slightly thickened and smoothly rounded. As determined from the right cheek, the channel is floored by the quadratojugal posteriorly and the jugal anteriorly. The squamosals are fragmentary in BSPHM XV 20, but essentially complete in FMNH PR 1760. They form the entire posterior margin of the temporal fenestra, from which they extend posteriorly, expanding gradually ventrally, to reach the occipital margin of the cheek. The entire dorsal and posterior margins of the squamosal, including a long, narrow anterior extension overlapped by the posterior process of the postorbital, bend abruptly medially to form a narrow occipital flange. The medial surface of the squamosal in the region of the posterior margin of the cheek contacts the posterodorsal edge of the quadrate ramus of the pterygoid. The occipital flange of this portion of the squamosal wraps around the posterior edge of the quadrate ramus of the pterygoid and is in turn overlapped externally by the supratemporal and tabular. The remaining ventral portion of the occipital flange of the squamosal wraps around the posterior edge of the quadrate and is entirely visible in posterior view. Both the quadrate and the quadrate ramus of the pterygoid, therefore, support the occipital margin of the cheek. The splint-like supratemporal is pointed at both ends, but its posterior half appears to be slightly wider. The anterior half of the bone is seated in a shallow groove on the end of the posterolateral wing of the parietal, whereas the posterior half angles ventrally to overlap the squamosal.



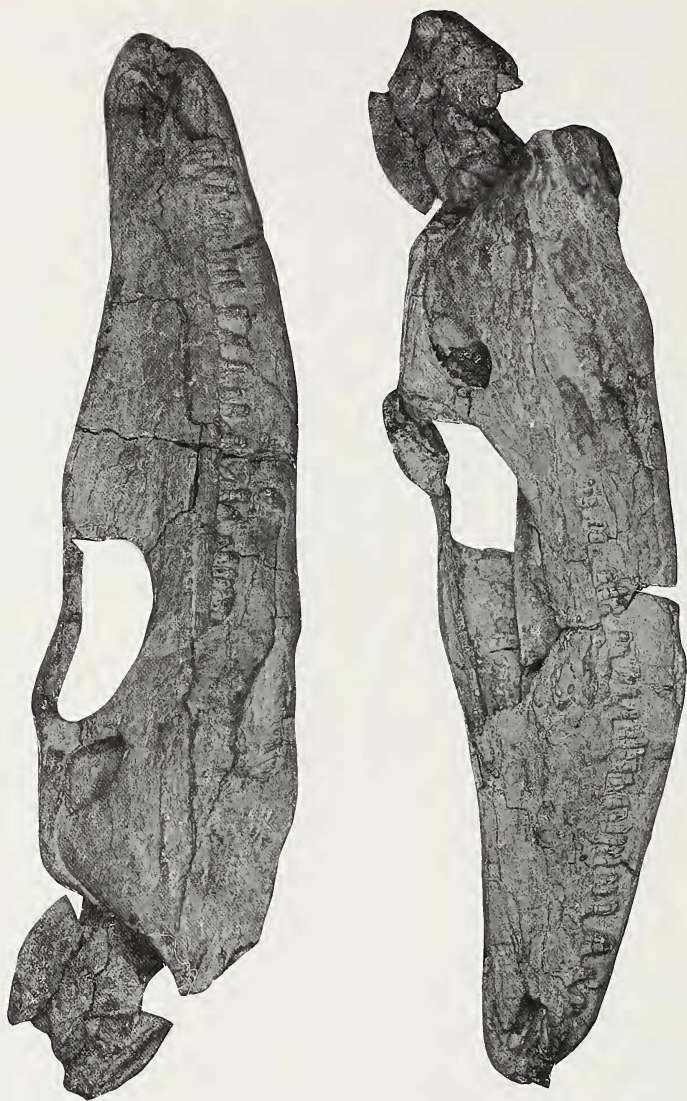


Fig. 10.—*Varanosaurus acutirostris*, FMNH PR 1760. Lateral views of skull with attached lower jaws. Scale as in Fig. 11.

The tabulars are present in both skulls BSPHM XV 20 and FMNH PR 1760, but details of their morphology are best preserved in the latter. The tabular occupies the dorsolateral corner of the occipital surface of the skull, and its nearly flat surface faces posteriorly, dorsally, and medially. Dorsolaterally the tabular contacts the medial margins of the posterolateral wing of the parietal and the central portion of the supratemporal. A short, rectangular, medial portion of the tabular contacts the entire lateral margin of the postparietal. At the lateral edge of its free posteroventral margin there is a deep, dorsally arching, semicircular notch, the lateral border of which is extended by the distal end of the supratem-



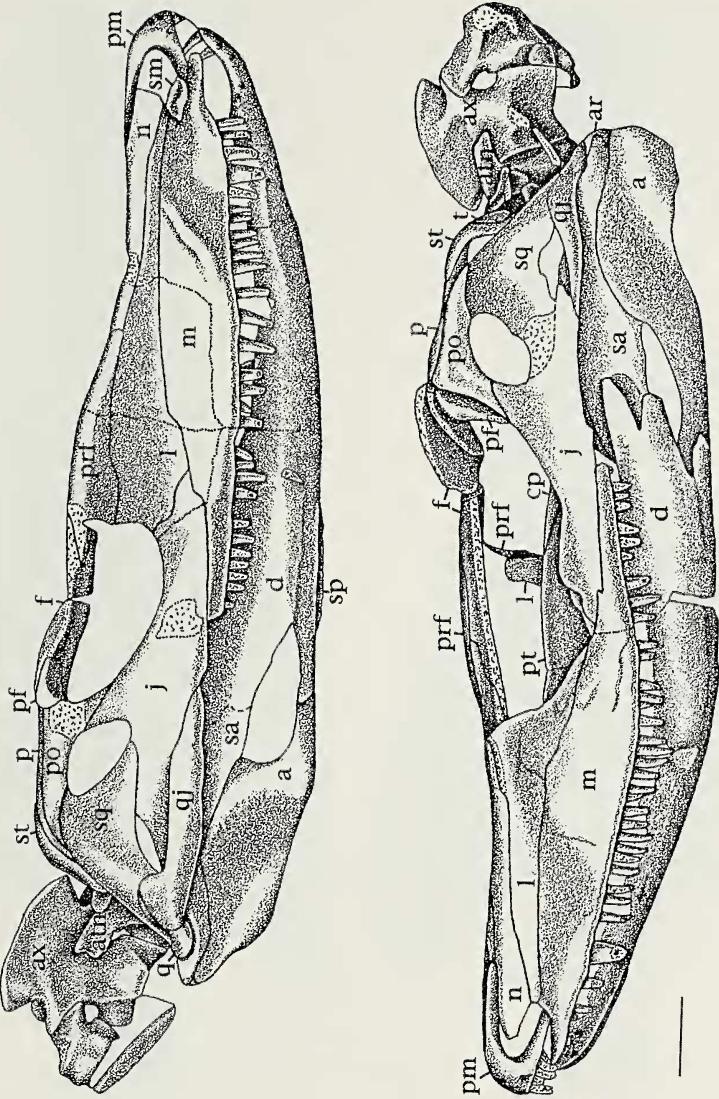


Fig. 11.—Illustration of *Varanosaurus acutirostris*, FMNH PR 1760 as seen in Fig. 10. Scale = 1 cm.

poral. There is considerable thickening of the tabular toward its medial contact with the supraoccipital. The tabular does not extend ventrally below the supraoccipital and, therefore, does not contact the opisthotic. As a result, the posttemporal fenestra is not closed laterally.

*Palate.*—The structure of the vomer and the internal naris is best seen in the partial snout FMNH UC 34. In this specimen the very narrow vomer widens gradually posteriorly to about three times its anterior width, as it forms all but a small anterior portion of the medial margin of the internal naris. The slightly concave, lateral narial margin of the vomer turns abruptly dorsally to form a low flange with a smoothly rounded rim which attains a greatest height of about 1.3

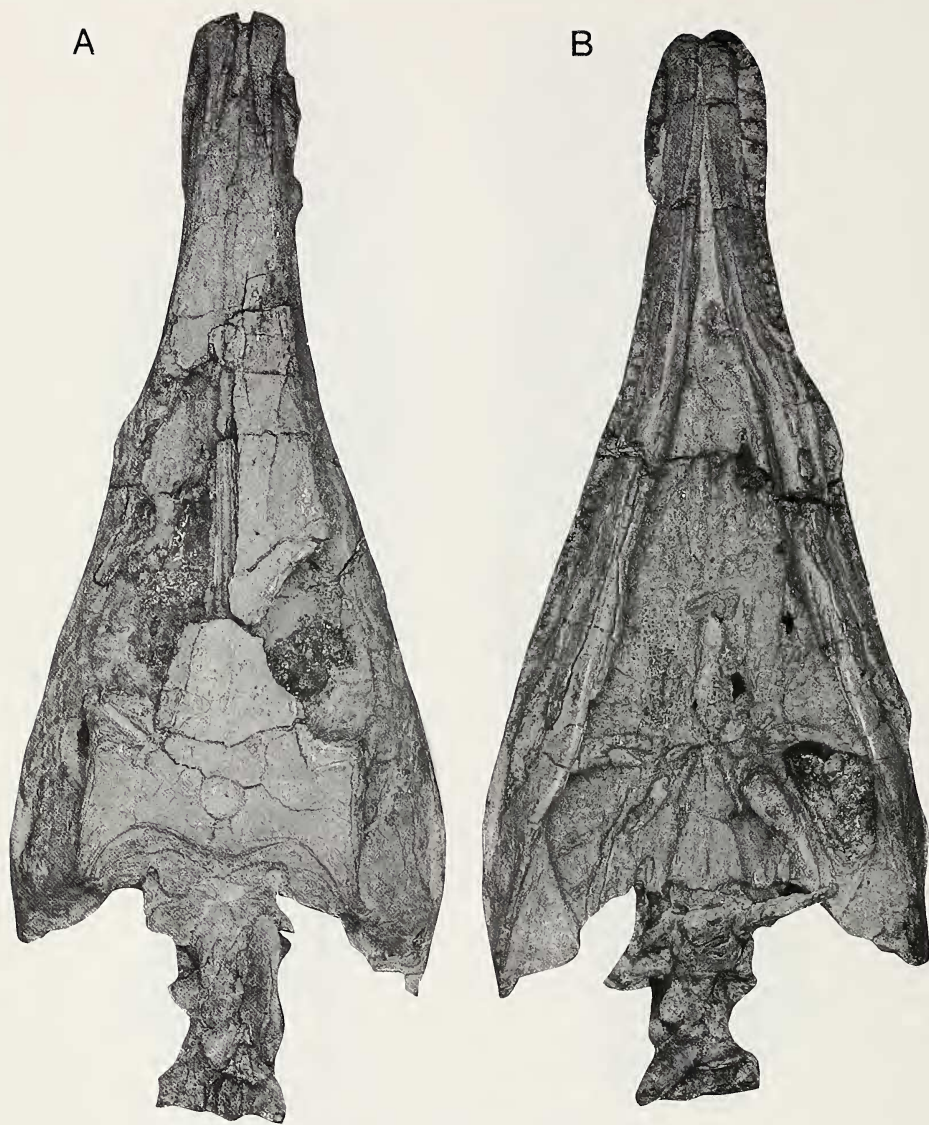


Fig. 12.—*Varanosaurus acutirostris*, FMNH PR 1760. A, dorsal, and B, ventral (palatal) views of skull with attached lower jaws. Scale as in Fig. 13.

mm near its posterior end. A small, posteriorly-directed vomerine process of the premaxilla completes the anterior end of the medial margin of the internal naris. It is not possible to determine precisely the sutural relationships between the vomer and palatine. It appears, however, that the palatine had a very narrow contact with the posterior end of the lateral margin of the vomer on the border of the internal naris. A single row of small teeth supported by a low ridge lies close to and parallel with the medial margin of the ventral surface of at least the posterior half of the vomer. Close to and parallel with the medial edge of the dorsal surface of the vomer is a vertical, ascending flange, that reaches a maximum



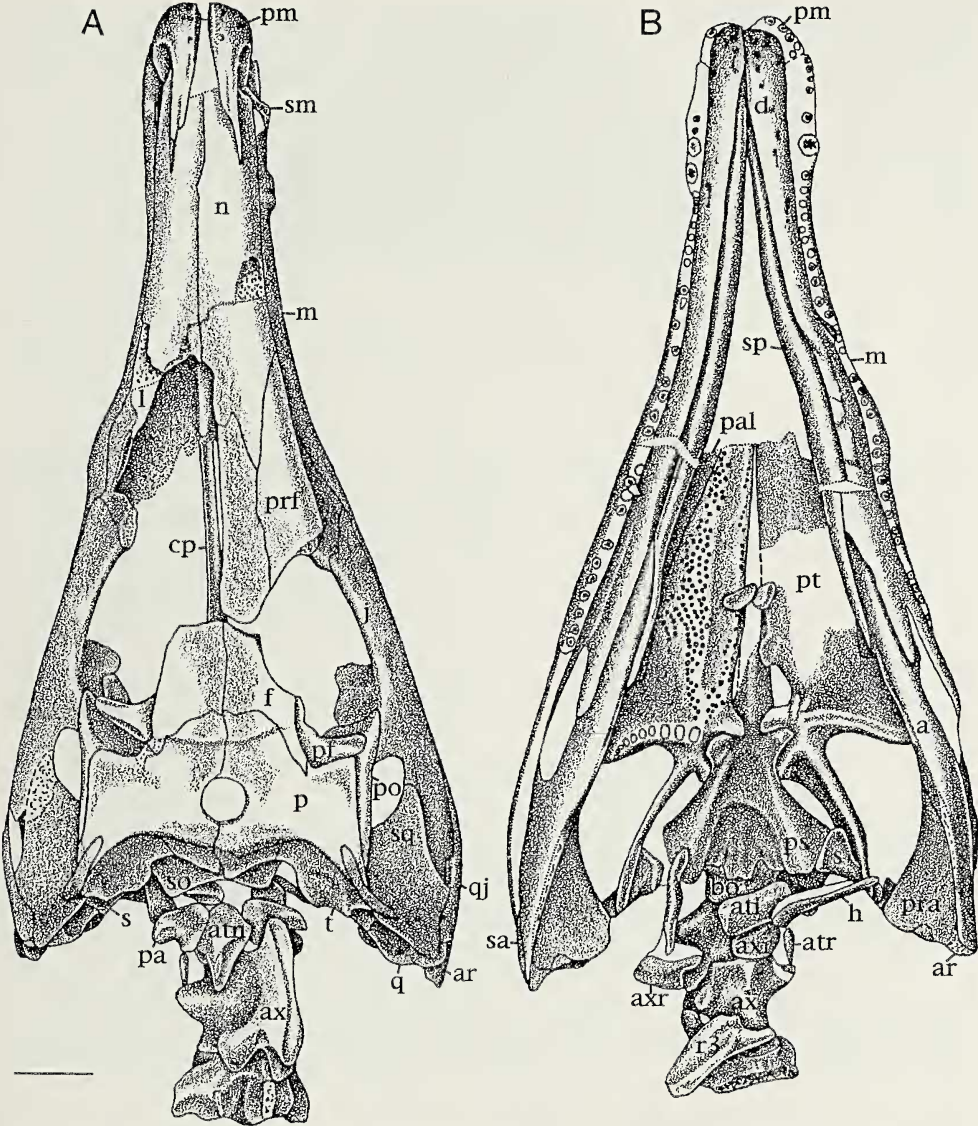


Fig. 13.—Illustration of *Varanosaurus acutirostris* FMNH PR 1760 as seen in Fig. 12. Scale = 1 cm.

height of about 3.3 mm. Clasped between approximately the posterior third of the ascending flanges of the paired vomers are the distal ends of the anterior rami of the pterygoids.

Although paired palatines are present in both skulls, only the right in FMNH PR 1760 is exposed partially in dorsal and ventral views. The exposed posterior portion of the palatine can be clearly defined in ventral view. It obviously had a narrow, anteriorly tapering, band-like exposure along the lateral margin of the palate between the ectopterygoid and the posterior border of the internal naris. The actual medial extent of its width is greatly reduced in ventral view by an

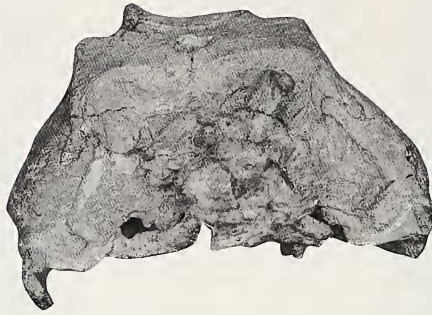


Fig. 14.—*Varanosaurus acutirostris*, FMNH PR 1760. Skull in posterior (occipital) view. Scale as in Fig. 15.

extensive overlap of the pterygoid. The palatine-ectopterygoid contact appears to angle posteromedially. Anteriorly the palatine overlaps dorsally the vomer for a short distance. The ectopterygoids are present in both skulls, but only those of the right side are well exposed in ventral view. In outline they are narrowly trapezoidal, with the medial and lateral margins being nearly parallel. The posterior and medial margins meet at nearly a right angle that is deeply incised into the lateral margin of the pterygoid. Approximately the posterior half of the lateral margin appears to enter the border of the subtemporal fenestra, with the remaining anterior portion contacting the medial surface of the alveolar shelf of the maxilla. Both the palatine and ectopterygoid lack teeth.

The pterygoids are essentially complete in both BSPHM XV 20 and FMNH PR 1760, although not all aspects of their structure are visible; only very small portions of the anterior ends are present in FMNH UR 34. The pterygoid is of the standard primitive amniote form, consisting of an anterior (palatal) ramus, transverse flange, and posterior quadrate ramus. From the level of the posterior margin of the ectopterygoid the anterior ramus dominates the palatal surface as a long rectangular band that narrows very slightly anteriorly. Although the course of the pterygoid-vomer contact on the palatal surface is indeterminate, it is likely that the pterygoid did not reach the internal narial border. The very small interpterygoid vacuity has the outline of a narrow spade. Anterior to the interpterygoid vacuity the medial edge of the anterior ramus quickly expands dorsally into

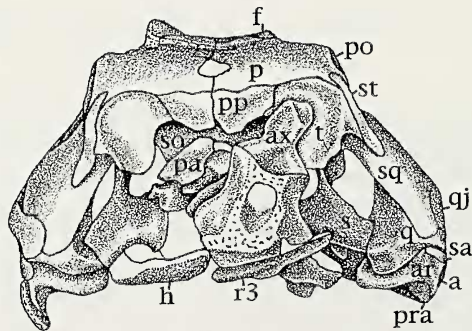


Fig. 15.—Illustration of *Varanosaurus acutirostris*, FMNH PR 1760 as seen in Fig. 14. Scale = 1 cm.



a nearly vertical ascending lamina. In FMNH PR 1760 the ascending lamina reaches its approximate maximum height of nearly 7 mm about 1 cm from its posterior end. The paired ascending laminae of the pterygoids unite with one another except for a very narrow portion along their dorsal borders which are reflected dorsolaterally so as to form a V-shaped trough that supports the base of the cultriform process of the braincase. In FMNH PR 1760 the medial ascending lamina of the pterygoid is exposed to about the level of the thirteenth postcanine tooth and undoubtedly continued further anteriorly. This is indicated in FMNH UR 34, where the medial ascending laminae end abruptly anteriorly at about the level of the fourth postcanine and the posterior margin of the internal naris. Here the laminae are clasped together between the dorsal ascending flanges of the vomers. This is well beyond the palatal exposure of the anterior ramus of the pterygoid, and as a result the anterior end of the medial ascending lamina must have had the appearance of a short, anteriorly-directed process. As best exemplified in FMNH PR 1760, the posterior end of the interpterygoid vacuity is closed on either side of the midline by a small, stout, triangular flange-like process (referred to here as the basal process) that projects posteromedially to nearly reach its mate. The basal process is twisted slightly about its long axis so that its superior surface, on which the basiptyergoid process of the braincase articulates, faces posterodorsally; this arrangement prevents ventral movement of the braincase relative to the palate. Because the epiptyergoid is not visible, its role in this joint is unknown.

The transverse flange of the pterygoid is quite massive and extends ventrally well below the level of the ventral rim of the skull. Its posterior margin lies at the level of the basiptyergoid articulation. The quadrate ramus extends posteriorly and slightly laterally as a thin, nearly vertical lamina to form the medial boundary of the subtemporal fenestra. It does not quite reach the dorsal process of the quadrate, although presumably it was in contact with the medial surface of an anterior extension of the quadrate. Anteriorly the quadrate ramus produces a short, posteromedially-directed flange just posterior to the basiptyergoid process. This flange, which may be called the postbasal process, forms the posterior wall of a deep socket into which the basiptyergoid process fits and would have prevented posterior movement of the braincase relative to the palate.

In FMNH PR 1760 very small teeth, mainly tooth bases, measuring about 0.06 mm in diameter, are distributed over most of the palatal ramus except for two edentulous areas, a narrow anteroposterior strip near the medial margin and a triangular region anterior to the transverse process. All that remains of the teeth of the transverse flange are the bases in FMNH PR 1760. Each flange supported a single row of about ten teeth, which gradually increase in size medially and whose bases tend to be anteroposteriorly oval.

*Braincase.*—The exoccipitals and basioccipital remain as distinct bones. The exoccipitals are partially exposed in both BSPHM XV 20, and FMNH PR 1760. They are very much like those of other Permo-Carboniferous synapsids, bounding all but the dorsal margin of the foramen magnum. Their expanded ventral bases meet to form the floor of the foramen, whereas a short intermediate, vertical pillar-like section and a dorsal wing-like portion that angles medially form the lateral margins. The exoccipitals are separated narrowly from one another dorsally, where the foramen magnum exhibits a moderately deep, semicircular, notch-like incisure into the supraoccipital. Neither the small openings for cranial nerve XII, located typically on the lateral surface of the basioccipital, nor the jugular foramen

for cranial nerves IX–XI, positioned on the exoccipital–opisthotic suture, can be discerned. The articular surface of the condyle is hidden from posterior view by the atlas–axis complex in both skulls. Ventrally the basioccipital is covered by the parasphenoid anterior to the neck of the condyle, except for a short, wide, midline projection onto the base of the neck. Anterior to the neck the lateral surface of the basioccipital flares abruptly laterally to form the posteromedial margin of the fenestra ovalis.

The thick, massive supraoccipital is well preserved and distinct from the opisthotics in both skulls. As exposed on the occiput it extends outward and slightly forward from the midline as broad, slightly arched, wing-like expansions. At its ventrolateral corner it forms the medial wall and ventral floor of the small, notch-like posttemporal fenestra, separating the ventromedial corner of the tabular and the dorsal margin of the paroccipital process of the opisthotic. The dorsolateral margin of the supraoccipital does not extend beyond the medial margin of the fenestra, and therefore can be considered to lack a lateral process. On the other hand, the supraoccipital does form the ventral floor of the posttemporal fenestra, as its contact with the opisthotic extends along the ventromedial lip of the fenestra. The supraoccipital continues a short distance anterodorsally beneath the postparietals. In occipital view the paroccipital process of the opisthotic is very short, extending barely, if at all, beyond the small posttemporal fenestra and terminating well short of the quadrate. The process is, however, very thick anteroposteriorly. Its proximal contact with the supraoccipital is a dorsolaterally straight line which extends to the ventromedial margin of the posttemporal fenestra.

Much of the dorsal portion of the prootics are exposed in BSPHM XV 20, but not visible in any of the figures given here. The prootics form the greater portion of the lateral walls of the braincase, with the dorsal margin steadily expanding in height posteriorly so that the dorsal portion of their posterior margin contacts the supraoccipital and tabular. Near the anterior end of the smoothly rounded dorsal margin a small semicircular notch marks the exit of the trigeminal nerve (V). Anteriorly the prootics converge slightly before ending in an anterodorsal contact with the processus sellares of the basisphenoids, with their lateral surfaces being smoothly continuous.

The fused basisphenoid and parasphenoid, the basiparasphenoid complex, is well preserved in both skulls, but each is exposed in differing aspects. The anterior cultriform process is well exposed in dorsal view in FMNH PR 1760, where it extends for a considerable distance anteriorly, apparently nearly reaching the level of the posterior border of the internal naris. For most of its length the cultriform process in FMNH PR 1760 is extremely narrow, with a V-shaped cross-sectional structure that becomes somewhat U-shaped anteriorly. In BSPHM XV 20 the lateral walls of the process are relatively much higher, and the trough-like midline groove between them supports the ventral edge of the sphenethmoid. The basiptyergoid processes are well preserved in FMNH PR 1760, where they appear as stout, subrectangular plugs that project ventrolaterally and slightly anteriorly and have a slightly convex articular facet on their distal surface. Posterior to the basiptyergoid processes the basiparasphenoid expands greatly laterally. In ventral view the lateral borders of the expansion are dominated by well-developed cristae ventrolaterales. These broadly triangular crests taper anteriorly to a narrow ridge and merge to form a concave posteromedial border between them. The wide, deeply depressed, triangular area separating the cristae even undercuts them slightly posteriorly. A short distance posterior to the union of the cristae there is an



abrupt, transverse, dorsalward step-like increase in the depth of the depressed area between them. In this region the parasphenoid is very thin and applied to the basioccipital as closely spaced, longitudinal striae.

The basiparasphenoid complex is partially exposed in dorsal view in BSPHM XV 20. The basisphenoid appears to be the sole contributor to the formation of the dorsum sellae. High, well-developed processus sellares of the basisphenoid form the lateral walls of a deep, smoothly finished, hemispherical depression of the retractor pit for the origin of the retractor bulbi and bursalis muscles. The anterior margins of the processus sellares form smoothly rounded, pillar-like structures that thicken slightly as they slope posterodorsally and slightly laterally to contact the prootics. Posteriorly the internal walls of the processes curve abruptly medially to form a continuous wall that is the dorsum sellae proper. This structure separates the anterior retractor pit from the posterior cranial cavity. The dorsum sellae in *Varanosaurus* closely approximates that in the varanopseid *Aerosaurus* (Langston and Reisz, 1981), but contrasts with that in *Dimetrodon* and possibly other early synapsids, where it is formed mainly, if not entirely, by the prootics (Romer and Price, 1940). The floor of the retractor pit is divided by a weak, longitudinal ridge that becomes more pronounced posteriorly, as it extends onto the anterior surface of the dorsum sellae.

The sphenethmoid is present as an ossified element in BSPHM XV 20, where it is positioned in the dorsal midline channel of the cultriform process. Except for lacking a small portion along its posterior margin it is undoubtedly complete, although only a portion of its posterior lateral surface is exposed.

*Stapes.* — The stapes are complete in BSPHM XV 20 and FMNH PR 1760, but only in the latter do both stapes appear to be undistorted and in their original positions. In BSPHM XV 20 the cheek + suspensorium has been laterally compressed, and both stapes with it. In consequence, little of the left stapes is visible except for part of the shaft; the right stapes is exposed in mostly posteromedial view. Its head is approximately in natural position, but the shaft has been bent posteriorly and medially. The *Varanosaurus* stapes closely resembles that of *Ophiacodon* (Romer and Price, 1940; Lombard and Bolt, 1988), although it is relatively smaller than the *Ophiacodon* stapes, particularly the length of the shaft. The large footplate is roughly oval, narrower ventrally, and more broadly rounded dorsally. The shaft is compressed strongly anteroposteriorly, and is slightly thicker ventrally than dorsally. The posterior opening of the stapedia canal is on the ventral margin of the shaft and adjacent to the head. The shaft runs ventrolaterally and posteriorly to reach the quadrate. In FMNH PR 1760 it lies in a vertical plane that is at about 45° to the sagittal plane. The distal end of the shaft fits into a distinct recess in the medial surface of the quadrate just dorsal to the condyle, but falls short of the floor of the recess, suggesting a possible cartilaginous continuation. A large dorsal process arises from the dorsal surface of the stapedia shaft just distal to the footplate and separated from it by a broadly rounded incisure. The dorsal process is markedly compressed, some 4 mm in anteroposterior extent, and appears to terminate in a slight expansion like that in *Ophiacodon*. With the stapes in natural position the dorsal process lies in an approximately parasagittal plane; its posterior edge runs nearly straight dorsoventrally and stands at a right angle to the upper border of the shaft. The dorsal process clearly contacts the underside of the tabular, just lateral to the tabular-supraoccipital contact. The inner surface of the tabular forms a thick boss along its contact with the dorsal process. This contact between the tabular and the dorsal process

in *Varanosaurus* was very short. Even assuming a cartilaginous continuation, the paroccipital process could not have extended laterally very far beyond the ossified portion seen in both BSPHM XV 20 and FMNH PR 1760.

*Mandible.*—The dentary is exposed essentially only on the lateral surface of the jaw, where it is the dominant element, occupying about 75% of the mandibular length. It is very slender and bowed broadly ventrally, and tapers gradually anteriorly to a very narrow symphysis. The posterior end forms the anterior half of the external mandibular foramen. Here the dorsal margin of the dentary continues a short distance posterodorsally in a shallow groove on the lateral surface of the surangular as a short, spike-like process that fails to reach the dorsal margin of the low coronoid eminence. Only in BSPHM XV 20 can the number of the dentary teeth be roughly estimated, where they are partially obscured by the upper jaw dentition. The dentary has 60 or slightly more tooth positions, and the teeth appear to have the same morphology as those of the upper jaw, but show little size variation. The series apparently reaches its greatest height at about its mid-length and decreases slightly more toward the posterior than the anterior end of the series, with the first four or five being slightly smaller than the largest teeth of the series.

The angular has a large, horizontally oval exposure on the posteroventral angle of the lateral surface of the jaw. Anteriorly it forms the posterior half of the ventral margin of the external mandibular foramen before continuing a short distance farther beneath the dentary as it tapers to the ventral margin of the jaw. Posterior to the foramen the entire dorsal margin of the angular contacts the surangular. It has a short, spike-like, posterodorsally-directed end that overlaps the lateral surface of the articular. The surangular forms the low, flat coronoid eminence which diminishes anteriorly as a short spike-like extension. It covers the posterior coronoid laterally except for a very narrow exposure of the latter along the anterior margin of the coronoid eminence. The narrow, rounded posterior end of the surangular angles upward as it overlaps the lateral margin of the articular. Only a very narrow margin of the posterodorsal end of the articular is visible in lateral view.

The splenial is the dominant element of the jaw in medial view, covering essentially its anterior half. As its posterior end tapers to the ventral margin of the jaw, it first contacts the narrow anterior end of the posterior coronoid, then broadly contacts the prearticular and angular. Although the anteriormost end of the splenial is not visible, it appears to have closely approached but not entered the jaw symphysis. From its lateral exposure the angular wraps around the ventral margin of the jaw in a sharp, modest keel, where it forms a narrow band along its posteroventral angle. The long, nearly straight contact with the prearticular dorsally is interrupted near its anterior end by the small inframandibular foramen. There is no development of the ventral keel of the angular into a reflected lamina, as seen in certain early synapsids. The long, narrow prearticular forms the broadly concave ventral border of the adductor fossa, then continues anteriorly to wedge sharply between the posterior coronoid and splenial. Near its posterior end the prearticular expands dorsally into a broadly triangular flange that curves medially to underlie the articular. *Varanosaurus* presumably possessed two coronoids, as do all early synapsids where this component is known, but only the posterior coronoid is visible in the specimens at hand. The anterior coronoid is typically a long, thin element that extends along the central portion of the medial surface of the alveolar shelf of the dentary. The posterior coronoid extends a short distance



along the posterior end of the medial surface of the alveolar shelf to the anterior margin of the adductor fossa. It then continues posterodorsally as a narrow strip that overlaps the medial surface of the surangular along the anterior margin of the coronoid eminence.

The articulars are present only in FMNH PR 1760, but little can be said about them because the lower jaws are tightly joined to the skull. There is a small, poorly defined retroarticular process which is supported by the angular and surangular, and the cotylus for the quadrate faces dorsally and possibly slightly medially.

#### PHYLOGENETIC RELATIONSHIPS

Until recently, the classification and interrelationships of Permo–Carboniferous synapsids presented by Romer and Price (1940) and Romer (1956) were widely accepted. Using explicitly cladistic methods of analysis, Reisz (1980) and Brinkman and Eberth (1983) presented hypotheses of relationships of Permo–Carboniferous synapsids that, although somewhat different from one another, radically altered earlier phylogenies. Differences between these two analyses were later resolved by Reisz (1986) and Reisz et al. (1992). These analyses, however, left the familial assignment of *Varanosaurus* unsettled. Romer and Price (1940) dealt extensively with *Varanosaurus* in their review of Permo–Carboniferous synapsids and resolved many of the taxonomic and phylogenetic problems associated with this genus: *Poecilospondylus*, based on a partial skeleton described by Case (1910), was recognized as a junior synonym of *Varanosaurus*; *Varanops brevirostris*, incorrectly assigned originally by Williston (1914) to *Varanosaurus*, was placed in a distinct new family, Varanopseidae; *Varanosaurus*, *Clepsydrops*, and *Ophiacodon* were united in the family Ophiacodontidae, and a strong similarity was recognized between *Varanosaurus* and *Ophiacodon*, particularly in the skull. Romer and Price (1940:22) also emphasized the importance of *Varanosaurus* as a “primitive pelycosaur,” viewing it as a primitive representative of the “ophiacodontoid assemblage.” Although aware of its many cranial similarities to *Ophiacodon*, in his review of this group Reisz (1986) placed *Varanosaurus* in Synapsida incertae sedis, arguing that the distinctive vertebral structure of the swollen neural arches, and differences in the atlas–axis complex and the tarsus makes assignment to Ophiacodontidae questionable. However, after a detailed restudy of the axial skeleton of *Varanosaurus*, Sumida (1989:457) concluded that there exist strong enough similarities to “argue for some relationship between *Varanosaurus* and ophiacodonts, but determination of the degree of such a relationship cannot be evaluated solely on the basis of vertebral structures described here.”

The present redescription of the cranial anatomy of *Varanosaurus* has prompted us to reconsider the phylogenetic relationships of this genus. In light of our current knowledge of Permo–Carboniferous synapsids, the following terminal taxa have been chosen as most suitable for standard cladistic analysis:

*Suborder Caseasauria*.—The eothyridid *Eothyris*, a small synapsid represented by a single, nearly complete skull, and the caseid *Cotylorhynchus*, a large herbivorous synapsid represented by several skeletons, have been used to infer the ancestral condition for this taxon. Specimens of these taxa were restudied by one of us (RR).

*Family Varanopseidae*.—*Mycterosaurus* and *Aerosaurus*, most recently described by Berman and Reisz (1982) and Langston and Reisz (1981), respectively, have been used to infer the ancestral condition for this family.

*Family Edaphosauridae*.—The ancestral condition of this family is inferred on

the basis of *Ianthasaurus* and *Edaphosaurus*, which have been described most recently by Modesto and Reisz (1990) and Modesto (1991), respectively.

*Haptodus garnettensis*.—This species was recently redescribed by Laurin (1993) and has been included because of its importance among Permo–Carboniferous synapsids, as it is considered to be the sister taxon to *Sphenacodontoidea* (Reisz et al., 1992).

*Superfamily Sphenacodontoidea*.—*Sphenacodon*, *Dimetrodon*, and *Biarmosuchus* have been used to infer the ancestral condition for this synapsid group (Reisz et al., 1992).

*Ophiacodon* and *Archaeothyris*.—These ophiacodontid genera have been included in this analysis not only because they have been cited as close relatives of *Varanosaurus*, but also because their skeletons are relatively well known. *Archaeothyris* has been described by Reisz (1972, 1975), and, although *Ophiacodon* has been described in great detail by Romer and Price (1940), excellent, recently collected specimens of *Ophiacodon* from New Mexico and Texas were also available for this study. Other ophiacodontids, such as *Clepsydrops*, *Stereorhachis*, and *Stereophallodon* are represented by fragmentary skeletal remains and are too poorly known to be useful in the present analysis.

For the purpose of the present phylogenetic analysis of the above taxa, 95 osteological characters or features were used (Appendix 1). The majority of these characters have been employed in previous synapsid studies (Gauthier et al., 1988; Reisz, 1986; Reisz et al., 1992), but new characters have also been included, mainly as a result of the present study of *Varanosaurus* and its nearest relatives. The data matrix (Appendix 2) that includes these characters was subjected to the branch and bound algorithm of PAUP 3.0, which guarantees to find all the most parsimonious trees. The analysis was performed on a Macintosh II SI, using the Macintosh version of PAUP 3.0 (Swofford, 1989). In this analysis the trees were rooted using the outgroup method, and the character-state optimization employed was delayed transformation (DELTRAN). The character states were left unordered. Only one most parsimonious tree was found (Fig. 16), having a tree length of 158 steps and an overall consistency index of 0.785 (0.717 when uninformative characters were excluded). The results of the analysis indicate that *Archaeothyris*, *Ophiacodon*, and *Varanosaurus* form a clade, here designated as the Family Ophiacodontidae, and that *Ophiacodon* and *Varanosaurus* share a more recent common ancestor than either does with *Archaeothyris*. In addition, *Edaphosauridae*, *Haptodus*, and *Sphenacodontoidea* also form a clade. The latter clade, together with *Varanopseidae* and *Caseasauria*, are outgroups or progressively more distant sister taxa to Ophiacodontidae. The shared derived characters, or synapomorphies, used to distinguish taxa and to determine relationships among them are indicated by an Arabic number enclosed in square parentheses; a character number preceded by a minus sign indicates that it is a reversal. Some patterns of synapomorphy, when analyzed, were determined to be ambiguous in that more than one transformational series was equally parsimonious; in these instances the characters are denoted by an asterisk after the character number. The character states are indicated by parentheses bracketing Arabic numbers (0–3), denoting unordered states.

The results of the analysis support the hypothesis that *Varanosaurus* forms a clade with *Ophiacodon* and *Archaeothyris*, the Ophiacodontidae. This relationship is supported by the following synapomorphies:

*Antorbital region is elongate, at least twice as long as the postorbital region* [2].



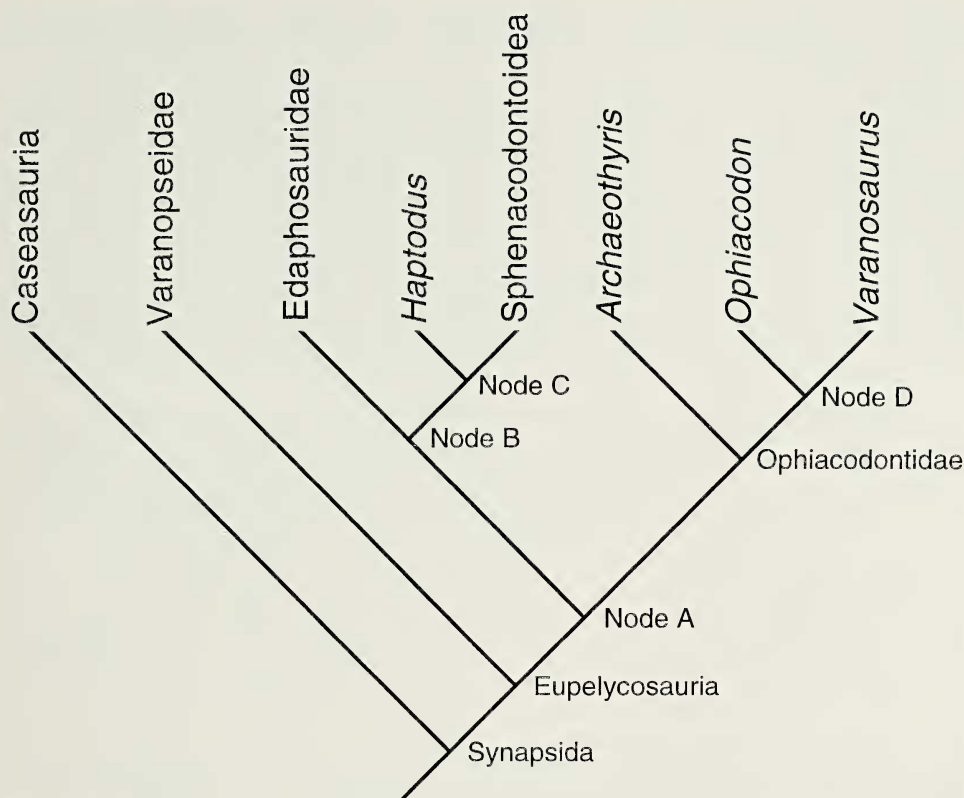


Fig. 16.—Cladogram illustrating hypothesis of phylogenetic relationships of ophiacodontid synapsids. Autapomorphies defining Node A: 8, 19, 22, 28, 29, 37(2), -38, 40, 45, 47, 49, 60, 72, 84, and 88; Node B: 14, 27, 30\*, 31\*, 32\*, 39(2), 42(2)\*, 46(2)\*, 51\*, 61, 62, 63\*, 73, 79\*, 80\*, 85\*, 91, 96; Node C: 3, 6(2)\*, 12\*, 20, 21, 33, 50, 56, 71, 75(2), 82, 92, 93, 95\*; Ophiacodontidae: 2, 9, 33(2), 42\*, 54, 55, 56(2), -69\*, 74, 76, -89, -90\*; Node D: 4, 6\*, 12\*, 16, 31\*, -37, 44\*, 46\*, 51(2)\*, 53\*, 57\*, 63\*, 65, 67, 72\*, 83\*; *Varanosaurus*: 1, 5, 7(2), 17\*, 26\*, 36,, 38, 58, 68, 92. When the commonality of a character is unknown because of missing data, the character has been placed in the smallest clade in which it is found (DELTRAN optimization in PAUP) and, therefore, several characters could apply to a more inclusive clade than suggested here. Ambiguous status of characters is noted by an asterisk (\*) and reversals by a negative sign (-). A derived state other than "1" is indicated in brackets (2).

All ophiacodontids exhibit a marked elongation of the snout. The antorbital region, as measured from the anterior limit of the orbit to the end of the snout, is at least twice the length of the postorbital region, as measured from the posterior limit of the orbit to the posteroventral corner of the skull. All other taxa used in this study have the inferred primitive condition, even though some genera (e.g., *Dimetrodon* and *Sphenacodon*) have elongated snouts.

*Nasal is longer than frontal* [9]. In all members of the ophiacodontid clade the nasal bone is longer than the frontal (1). It is interesting, however, that this derived condition is found not only in *Archaeothyris*, where the frontal shows the primitive, unelongated condition, but also in *Ophiacodon* and *Varanosaurus*, where both the frontal and nasal bones are elongated. The primitive condition of short, subequal nasals and frontals (0) is found in all other taxa used in this study except *Sphenacodontidea*, where the nasal is significantly longer than the frontal. The

analysis indicates that this derived condition must have evolved independently in spenacodontoids.

*Maxillary supracanine buttress has ascending process* [33]. The primitive condition of no supracanine maxillary buttress (0) is seen in caseasaurians, varanopseids, and edaphosaurids. One of two derived conditions, the presence of a buttress without an ascending process (1), distinguishes the clade of *Haptodus* and spenacodontoids. The second derived condition of a supracanine maxillary buttress, an ascending process (2) that extends to, or nearly to, the dorsal limit of the maxilla, is found in all members of the ophiacodontid clade. In *Archaeothyris* and *Varanosaurus* the ascending process is a broadly rounded ridge that is not set off sharply from the medial surface of the maxilla, whereas in *Ophiacodon* the ascending process is a narrow, sharply defined ridge on the medial surface of the maxilla.

*Ventral margin of postorbital region of the skull is formed by slightly concave quadratojugal* [42\*]. The ventral margin of the postorbital region of the skull is nearly straight and formed by the quadratojugal (0) in caseasaurians and varanopseids, the inferred primitive state for synapsids, whereas in ophiacodontids this portion of the ventral edge of the skull differs in exhibiting the derived condition of being slightly concave (1). In edaphosaurids, *Haptodus*, and spenacodontoids the quadratojugal does not contribute to the ventral margin of the postorbital region of the skull, and the ventral margin is strongly concave (2). This pattern of distribution makes the derivation of this synapomorphy in ophiacodontids ambiguous, since it is equally parsimonious to derive it from either state (0) or (2).

*Paroccipital process of opisthotic is short* [54]. All known ophiacodontids have short, knob-like paroccipital processes (1), whereas in all other synapsids used in this study the process is well developed and long (0). The presence of a long paroccipital process appears to be the primitive character state for synapsids, as well as for other Permo-Carboniferous reptiliomorph and amniote taxa. It is not understood why ophiacodontids appear to have reduced the length of the paroccipital process in a manner similar to that of protorothyridids and possibly millerettids (Carroll, 1982).

*Tabular does not extend to the level of the ventral edge of the supraoccipital* [55]. With the only known exceptions being the ophiacodontids, in all Permo-Carboniferous synapsids the tabular is greatly expanded ventrally to form a wing-like structure that extends well below the level of the supraoccipital to contact the distal end of the paroccipital process of the opisthotic and enclose the posttemporal fenestra laterally (0). In *Ophiacodon* and *Varanosaurus* the tabular is greatly shortened ventrally and does not extend to the level of the ventral margin of the supraoccipital (1). Whereas in *Varanosaurus* this results in the posttemporal fenestra being open laterally, in *Ophiacodon* the opisthotic has become greatly expanded dorsally not only to contact broadly the tabular, but apparently to obliterate the posttemporal fenestra or possibly displace it to the lateral margin of the occiput. It is impossible to determine without question the state of this character in *Archaeothyris* in that the occiput, preserved only in the holotype, is incomplete and the tabular is not preserved. In the description (Reisz, 1972) of *Archaeothyris* the opisthotic was misidentified as the exoccipital. The opisthotic appears to be similar to that in *Varanosaurus* in having a distinct but short, knob-like paroccipital process. Therefore, a posttemporal fenestra is likely to have been present in *Archaeothyris*, but it cannot be determined whether or not it was



bounded laterally by the tabular. The abbreviated paroccipital process of *Archaeothyris*, however, may indicate that, as in *Varanosaurus*, it was not in contact with the tabular.

*Paroccipital process of opisthotic is robustly constructed due to an anteroposterior thickening* [56]. In Permo–Carboniferous synapsids the paroccipital process is primitively a broad, blade-like structure as in caseosaurs, varanopseids, and edaphosaurids (0). Two derived conditions can be recognized: in *Haptodus* and sphenacodontoids the blade-like paroccipital process is relatively narrow (1), especially when compared to the primitive condition; the second derived condition occurs in ophiacodontids, where the short paroccipital process is not blade-like, but rather has become robust due to an anteroposterior thickening (2). Our analysis indicates that the two derived conditions evolved independently from the primitive state.

*Maxilla has more than four precanine teeth* [–69\*]. In both *Ophiacodon* and *Varanosaurus* there are numerous precanine maxillary teeth, ranging from five to 11 (0). In the holotype of *Archaeothyris* only a fragment of the caniniform region is preserved, but a referred specimen (Reisz, 1975) indicates clearly that there are more than four precanine maxillary teeth. In a second referred specimen (Reisz, 1972:fig. 4B) there appear to have been only three precaniniform maxillary teeth, but the anterior end of the maxilla is incomplete and generally poorly preserved. Other Permo–Carboniferous synapsids, including *Haptodus* and sphenacodontoids, have four or fewer precanine maxillary teeth (1). This character, however, is difficult to evaluate in three groups of synapsids—the varanopseids, caseids, and edaphosaurids—because they lack distinct caniniform teeth. In *Mycterosaurus* there are four tooth positions in the area anterior to the caniniform region, and in *Aerosaurus* there are also four teeth anterior to the caniniform region of the maxilla, probably indicating the presence of the derived condition (1). However, the two advanced varanopseids *Varanops* and *Varanodon* both possess long precaniniform regions, with as many as ten teeth. In both the caseid *Cotylorhynchus* and the edaphosaurid *Edaphosaurus* there is no caniniform region of the maxilla. The eothyrids *Eothyris* and *Oedaleops*, however, possess one and two precanine maxillary teeth, respectively, allowing us to code the caseosaurs as having the derived state of fewer than four precanine maxillary teeth (1). In the primitive edaphosaurid *Ianthasaurus* there are distinct canines and a long precanine maxillary region, allowing us to infer the primitive condition for the family (0). The distribution of the character states, therefore, suggests that the presence of more than four precanine maxillary teeth in the ophiacodonts is a reversal.

*Axial neural spine is expanded slightly beyond levels of the anterior and posterior edges of centrum* [74]. In all synapsids the axial neural spine is larger in its anteroposterior extent than any of the other spines of the cervical series. In the ophiacodontids used in this study the axial neural spine is greatly expanded anteroposteriorly, extending beyond the levels of the anterior and posterior limits of the axial centrum (1). In other Permo–Carboniferous synapsids the axial neural spine tends to extend only beyond the level of the anterior but not the posterior limit of the centrum (0).

*One of two sacral ribs attaches directly to the iliac blade* [76]. In all amniotes there are at least two sacral vertebrae. In caseids there are either three or four sacral vertebrae, and their ribs make direct contact with the iliac blade. In *Edaphosaurus* and sphenacodontoids the ribs of all three sacral vertebrae contact the ilium directly, as do the ribs of the two sacral vertebrae in varanopseids (0). On the other hand, in *Ophiacodon* and *Varanosaurus*, although both possess two

sacral vertebrae, only the greatly expanded rib of the first makes direct contact with the ilium. The second sacral rib actually contacts the posteromedial edge of the expanded first rib and provides additional support without directly contacting the ilium (1). We interpret this condition as an autapomorphy of ophiacodontids. In *Archaeothyris* there is no second sacral rib or vertebra preserved among the known specimens, but the shape and size of the preserved first rib indicates that the same condition prevails here as in the other ophiacodontids (Reisz, 1972:fig. 6F).

*Ilium possesses dorsal groove or trough* [−89]. Within synapsids there are two distinct morphologies in the dorsal region of the iliac blade immediately above the area of the sacral rib attachment. The inferred primitive state is the presence of a dorsal groove or trough (0) that may have served for the attachment of axial musculature (Romer, 1956). This character is seen only in ophiacodontids, whereas in all other Permo–Carboniferous synapsids the dorsal trough is absent (1). We interpret this as a character reversal, because the dorsal trough is present in diadectomorphs and several sauropsid taxa.

*Posterior process of ilium is slender and extends close to the level of the posterior limit of ischium* [−90]. In most Permo–Carboniferous amniotes the ilium has a slender posterior process that extends to or is close to the level of the posterior limit of the ischium. This is considered the primitive condition and is also found in *Ophiacodon* and *Varanosaurus* (0). In *Archaeothyris* most of the iliac blade is not preserved, but the shape of its base indicates that it must have been slender and posteriorly-directed, as in the other ophiacodontids. In all other Permo–Carboniferous synapsids there is evidence of a dorsal process of the ilium, and, although the posterior process may be well developed, it does not reach the level of the posterior margin of the ischium (1).

The analysis conducted here also indicates that *Varanosaurus* is more closely related to *Ophiacodon* than to *Archaeothyris*. This hypothesis of relationships is supported by the 15 synapomorphies described below:

*Posterior wall of orbit is formed by medial flange of jugal and postorbital* [4]. In both *Ophiacodon* and *Varanosaurus* the postorbital bar has a well-developed, medial, shelf-like orbital flange of the jugal and postorbital that forms the posterior wall of the orbit (1). The postorbital is not preserved in any of the known specimens of *Archaeothyris*, but one of the referred specimens (Reisz, 1972:fig. 4C) has a well-preserved jugal which lacks this feature, indicating that it retained the primitive condition of an absence of a posterior orbital wall formed by the jugal and postorbital (0). All other Permo–Carboniferous synapsids also lack a posterior wall of the orbit formed by the jugal and postorbital.

*Premaxilla is long and slender* [6\*]. Three different patterns of premaxillary proportions can be identified in Permo–Carboniferous synapsids. The body of the premaxilla is either short and relatively broad, as in eothyridids, caseids, varanopseids, and *Edaphosaurus* (0); slender and elongate, as in *Ophiacodon* and *Varanosaurus* (1); or robust and massive, as in *Haptodus* and sphenacodontoids (2). There is no available information on the premaxilla of *Archaeothyris*, making this synapomorphy of *Ophiacodon* and *Varanosaurus* ambiguous.

*Prefrontal has antorbital recess* [12\*]. The presence of a depression on the laterally facing surface of the prefrontal (1) near the anterodorsal corner of the orbit in *Ophiacodon* and *Varanosaurus* may be related to the lateral expansion of this element in front of the orbit. The presence of a similar, but shallower recess in *Haptodus*, and a deeper recess in sphenacodontoids makes this synapomorphy



ambiguous, as does the lack of information on the prefrontal in the primitive ophiacodontid *Archaeothyris*.

*Frontal has long anterior process* [16]. In Permo–Carboniferous synapsids the frontal has a supraorbital contribution which separates the bone into distinct anterior and posterior processes. Primitively these processes are subequal (0), as in all caseasaurians, *Mycterosaurus*, edaphosaurids, *Haptodus*, and *Archaeothyris*. In *Ophiacodon* and *Varanosaurus*, however, the anterior process of the frontal is significantly longer than the posterior process (1). Sphenacodontids such as *Dimetrodon* and *Sphenacodon* also show the derived state, but it is interpreted as having been derived independently from that in ophiacodontids.

*Ventral edge of maxilla is slightly convex* [31\*]. The ventral margin of the maxilla is straight in caseasaurians, varanopseids, and *Archaeothyris*, representing the primitive condition (0) among Permo–Carboniferous synapsids, whereas the slightly convex margin in *Ophiacodon*, *Varanosaurus*, edaphosaurids, and *Haptodus* (1), and the strongly convex margin in sphenacodontoids (2) are considered derived states. This pattern of distribution makes the derivation of the synapomorphy uniting *Ophiacodon* and *Varanosaurus* ambiguous, because it is equally parsimonious, on the one hand, to acquire the derived state (1) in both the ophiacodontid clade and the clade uniting edaphosaurids, *Haptodus*, and sphenacodontoids, as it is to acquire the derived state (1) once in the clade uniting ophiacodontids, edaphosaurids, *Haptodus*, and sphenacodontoids, with a reversal to the primitive state in *Archaeothyris*; either scenario would require a total of two steps.

*Jugal has narrow contribution to ventral edge of skull* [–37]. In both caseasaurians and varanopseids the maxilla contacts the quadratojugal, excluding the jugal from the ventral edge of the skull (0). In *Ophiacodon* and *Varanosaurus* the jugal has a narrow contribution to the ventral edge of the skull, whereas in *Archaeothyris* and all other Permo–Carboniferous synapsids there is a wide jugal contribution to the ventral edge of the skull (2). This pattern of distribution indicates that the character state in *Ophiacodon* and *Varanosaurus* is best interpreted as a character reversal from a wide (2) to a narrow (1) jugal contribution to the ventral edge of the skull.

*Palatine is narrow* [44\*]. Typically in Permo–Carboniferous synapsids the palatine is a well-developed, large bone which contributes significantly to the palatal surface (0). Although in *Ophiacodon* and *Varanosaurus* the palatine is a long element, its width in ventral view is greatly reduced by the overlapping pterygoid which forms most of the palatal surface (1). This synapomorphy is ambiguous only because the extent of the palatine in *Archaeothyris* is unknown.

*Medial shelf of the quadrate ramus of the pterygoid is narrow* [46\*]. Primitively in synapsids there is a large, medially directed shelf along the ventral margin of the quadrate ramus of the pterygoid (0), as seen in caseasaurians and varanopseids. In both *Ophiacodon* and *Varanosaurus* this shelf is reduced in width (1), whereas in edaphosaurs, sphenacodontoids, and *Haptodus* it is absent (2). However, because of the lack of any information regarding the structure of the pterygoid in *Archaeothyris*, this synapomorphy remains ambiguous.

*Laterally-directed basiptyergoid process contacts posterior margin of medially-projecting process of palate to restrict ventral movement of braincase relative to palate* [51\*]. Primitively in synapsids the basiptyergoid process of the braincase is large and oriented laterally, and there is no bony restraint of the pterygoid that would restrict the braincase from ventral movement relative to the palate (0). The basicranial articulation in *Ophiacodon* and *Varanosaurus* is unique among

synapsids in that the basiptyergoid process projects mainly laterally and extends along the posterior margin of a short, medially-projecting, knob-like palatal process formed by the pterygoid and possibly the epiptyergoid that prevents ventral movement of the braincase relative to the palate (2). Typically in other Permo-Carboniferous synapsids the basiptyergoid process projects strongly anteriorly, with its distal end abutting directly against that of a complementary process formed in varying degrees by the pterygoid and epiptyergoid (1). This synapomorphy is ambiguous because the braincase is unknown in *Archaeothyris*.

*Depth of depressed area between cristae ventrolaterales is abruptly increased posteriorly by a transverse, step-like dorsal elevation of the parasphenoidal plate* [53\*]. Among Permo-Carboniferous synapsids only in *Ophiacodon* and *Varanosaurus* is the depth of the depressed area between the cristae ventrolaterales of the braincase abruptly increased posteriorly by a transverse, step-like dorsal elevation of the parasphenoidal plate (1). Typically the parasphenoidal plate between the cristae ventrolaterales occupies a single horizontal plane (0). However, in the absence of any information on the nature of the parasphenoid in *Archaeothyris*, or any other described ophiacodontid, this synapomorphy remains ambiguous, because it may define a more inclusive clade.

*Lateral mandibular fenestra is present* [57\*]. A distinct lateral mandibular fenestra is present in both *Ophiacodon* and *Varanosaurus* (1), and its absence (0) in any of the other synapsids included in this study is therefore judged the primitive condition. Because of the lack of any information regarding this structure in *Archaeothyris*, this synapomorphy remains ambiguous.

*Posterior ventral edge of the angular is strongly convex* [63\*]. The ventral edge of the angular is nearly straight or only slightly convex near the level of the jaw articulation in caseosaurs, varanopseids, and *Archaeothyris* (0), but is strongly convex in *Varanosaurus*, *Ophiacodon*, *Haptodus*, edaphosaurs, and spheonacodontoids (1). However, this synapomorphy is ambiguous, because it is equally parsimonious to make it the derived state for the clade formed at Node A (Fig. 16) with a character reversal for *Archaeothyris*, or an independently derived character at Nodes B and D.

*Number of maxillary teeth exceeds 36* [65]. Maximum maxillary dental counts of 37 and 55 in *Ophiacodon* and *Varanosaurus*, respectively, is higher than in any other synapsid included in this analysis. In contrast, there are places for 28 or 29 teeth on the maxilla of *Archaeothyris*. Only one other synapsid, *Varanops*, approaches the high dental count in the above ophiacodontids, with as many as 33 or 34 maxillary teeth. The inferred primitive condition for varanopseids is, however, a far lower dental count, as *Mycterosaurus* possesses 23 and *Aerosaurus* 25 maxillary teeth.

*Marginal teeth are elongate and columnar for most of their length basally* [67]. Most Permo-Carboniferous synapsids have either simple, conical marginal teeth that are slightly recurved (0), or somewhat more specialized marginal teeth adapted to herbivory, such as in caseids and *Edaphosaurus*. Although the marginal teeth in *Ophiacodon* and *Varanosaurus* can be characterized as generally conical in shape, they are also more slender and elongate than those in other synapsids, as their diameter remains relatively constant throughout much of their basal length to give them a rather columnar aspect (1). The marginal teeth of *Archaeothyris* retain the primitive, simple, conical shape.

*Ectopterygoid teeth are absent* [72\*]. The presence of teeth on the ectopterygoid (0) is presumed to be the primitive condition in synapsids, inasmuch as it occurs



in caseasaurians, varanopseids, edaphosaurids, and *Haptodus*. The absence of ectopterygoid teeth (1) in both *Ophiacodon* and *Varanosaurus* may be related to the general slender configuration of their palates. Sphenacodontoids also lack ectopterygoid teeth, but their palatal surfaces are not reduced in relative width as in ophiacodontids. We interpret the presence of the derived condition in sphenacodontoids as having been acquired independently from the above ophiacodontoids. However, the absence of any information on the presence of ectopterygoid teeth in *Archaeothyris* makes this synapomorphy ambiguous.

*Ventral clavicular plate is narrow* [83\*]. The possession of a relatively straight, narrow clavicle with a small ventral plate is an important synapomorphy of *Ophiacodon* and *Varanosaurus* (1). With the exception of *Haptodus*, the clavicles of all other Permo–Carboniferous synapsids have large, expanded ventral plates (0), the presumed primitive character state for synapsids. In the absence of any clavicles among the specimens of *Archaeothyris*, however, this synapomorphy must be considered ambiguous.

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## APPENDIX 1

Description of the characters used in the phylogenetic analysis of *Varanosaurus*. Characters are listed in order of their location on the skull, mandible, and postcranial skeleton.

### Skull

1. Transverse section of the antorbital region of skull: lateral and dorsal surfaces of snout gently convex (0), or flat and separated by sharp ridges (1).
2. Antorbital region of skull: short and approximately equal to postorbital region (0), or elongate and at least twice as long as the postorbital region (1).
3. Ventral edge of premaxillary: straight (0), or sloping anteroventrally (1).
4. Medial orbital process of jugal and postorbital: absent (0), or present (1).
5. Premaxillary dorsal process: single (0), or bifurcate (1).
6. Premaxillary body: short (0), long and slender (1), or robust (2).
7. Lateral surface of septomaxilla: lies medial to lateral surfaces of surrounding elements of naris (0), large with partial facial exposure (1), or small with partial facial exposure (2).
8. Nasal: shorter than parietal at midline (0), or longer than parietal at midline (1).
9. Nasal: shorter or equal to frontal (0), or longer than frontal (1).
10. Premaxillary process of nasal: broad (0), or narrow (1).
11. Posteroventral narial process of nasal: absent (0), or present (1).
12. Antorbital recess of prefrontal: absent (0), or present (1).
13. Nasal–maxillary suture: absent (0), or present (1).
14. Lateral orbital lappet of frontal: absent (0), poorly developed (1), or extends far laterally (2).
15. Anterior process of frontal: equal in width to posterior process (0), or narrower than posterior process (1).
16. Frontal: short anterior process (0), or long anterior process (1).
17. Small, elongate fenestra on jugal–squamosal suture: absent (0), or present (1).
18. Postfrontal: occupies one-third of dorsal orbital rim (0), or is long anteroposteriorly (1).
19. Parietal length at midline: equal to one-fourth of skull roof length (0), or is less than one-fourth of skull roof (1).
20. Posterolateral wing of parietal: narrow (0), or broad (1).
21. Lateral edge of parietal: concave or straight (0), or convex (1).



22. Pineal foramen to parietal width ratio: 1:5 or more (0), or less than 1:5 (1).
23. Postfrontal–postorbital suture: straight (0), or incised by postorbital (1).
24. Pineal ridge: absent (0), or present (1).
25. Posterior process of postorbital: long (0), or short (1).
26. Postorbital–supratemporal contact: present (0), or absent (1).
27. Lateral surface of postorbital: flat (0), or recessed (1).
28. Posterior process of postorbital: broad (0), or narrow (1).
29. Postorbital to preorbital length ratio: subequal (0), or less than 1 (1).
30. Postparietal: paired (0), or fused (1).
31. Ventral margin of maxilla: straight (0), gently convex (1), or strongly convex (2).
32. Posterior extent of maxilla: extends to level of postorbital bar (0), to middle of orbit (1), or beyond postorbital bar (2).
33. Supracanine buttress of maxilla: absent (0), present (1), or present with ascending process (2).
34. Preorbital dorsal process of maxilla: absent (0), or present (1).
35. Lacrimal contact with external naris: present (0), or absent (1).
36. Lacrimal contact with external naris: broad (0), narrow (1), or absent (2).
37. Contribution of jugal to ventral edge of skull: excluded (0), narrow (1), or wide (2).
38. Posterior process of jugal: broad, dorsoventrally wide (0), or dorsoventrally narrow (1).
39. Anteroventral process of quadratojugal: long (0), short (1), or absent (2).
40. Contribution of squamosal to zygomatic arch: absent (0), or present (1).
41. Lower temporal fenestra: small (0), or enlarged dorsoventrally (1).
42. Ventral margin of postorbital region of skull: straight (0), gently concave with major contribution by quadratojugal (1), or strongly concave without contribution by quadratojugal (2).
43. Width of ventral surface of vomer: broad (0), or narrow (1).
44. Width of ventral surface of palatine: broad (0), or narrow (1).
45. Medial ascending lamina of the anterior ramus of pterygoid: low (0), or high (1).
46. Medial shelf of quadrate ramus of pterygoid: large (0), narrow (1), or absent (2).
47. Quadrate ramus of pterygoid: short (0), or long, occupying most of the subtemporal fossa's medial edge (1).
48. Posterior edge of quadrate: covered by squamosal, sometimes with quadratojugal contribution (0), or exposed posteriorly for most of its height (1).
49. Shaft of stapes: rod-like (0), or blade-like (1).
50. Relative position of basicranial articulation: at level with transverse flange of pterygoid (0), or posterior to transverse flange (1).
51. Basispterygoid process of braincase: large, laterally-oriented, and braincase not restrained from limited ventral movement relative to palate by process of pterygoid (0), small, directed anteriorly with distal end abutting against that of a complementary, posteriorly-directed palatal process of pterygoid (1), or small, laterally-oriented, and extends along posterior margin of short, medially-projecting, knob-like process of pterygoid that restrains braincase from ventral movement relative to palate (2).
52. Ventral plate of parasphenoid: broad, and flares posterolaterally (0), narrow (1), or narrow with deep median depression (2).
53. Posteroventral emargination of parasphenoid ventral plate: absent (0), or present (1).
54. Paroccipital process of opisthotic: well developed and long (0), or short and knob-like (1).
55. Ventral development of tabular: tabular expanded ventrally below level of ventral margin of supraoccipital to form wing-like structure that contacts paroccipital process and encloses posttemporal fenestra laterally (0), or tabular greatly shortened ventrally so as not to extend below level of the ventral margin of supraoccipital and encloses posttemporal fenestra laterally but may contact dorsally expanded opisthotic to obliterate posttemporal fenestra (1).
56. Paroccipital process of opisthotic: broad and blade-like (0), narrow and blade-like (1), or short and robust (2).

#### *Mandible*

57. Lateral mandibular fenestra: absent (0), or present (1).
58. Mandibular symphysis: formed by dentary and splenial (0), or only by dentary (1).
59. Lateral exposure of splenial: narrow (0), or broad anteriorly (1).
60. Posteroventral edge of angular: ridged (0), or keeled (1).
61. Coronoid region of mandible: slightly convex (0), or strongly convex (1).
62. Posterior medial surface of prearticular: nearly straight (0), or twisted (1).
63. Posterior ventral edge of angular: slightly convex (0), or strongly convex (1).
64. Retroarticular process: absent (0), present but formed by several bones (1), or formed only by articular (2).

*Dentition*

- 65. Number of maxillary teeth: 35 or less (0), or more than 36 (1).
- 66. Cutting edges of marginal teeth: absent (0), or present (1).
- 67. Morphology of marginal teeth: conical (0), or elongate with nearly constant diameter for most of their basal length (1).
- 68. Length of caniniform teeth: less than twice the length of largest maxillary teeth (0), or equal to or greater than twice the length of the longest maxillary teeth (1).
- 69. Number of precaniniform maxillary teeth: more than four (0), or four or fewer (1).
- 70. Number of premaxillary teeth: five or more (0), or fewer than five (1);
- 71. Vomerine teeth: present (0), or absent (1).
- 72. Ectopterygoid teeth: present (0), or absent (1).

*Postcranial Skeleton*

- 73. Intercentra 1 and 2: in contact ventrally (0), or separated by ventral extension of atlantal pleurocentrum (1).
- 74. Axial neural spine: expanded anteriorly beyond level of anterior edge of centrum (0), or expanded beyond levels of both ends of centrum (1).
- 75. Midventral margin of dorsal centra: rounded (0), ridged (1), or keeled (2).
- 76. Sacral ribs: at least two sacral ribs attached directly to ilium (0), or only first, greatly expanded sacral rib attached directly to ilium (1).
- 77. Dorsal neural spines: short (0), tall (1), or very tall (2).
- 78. Dorsal neural spines: blade-like in lateral view (0), or rounded in transverse section (1).
- 79. Dorsal neural arches: not excavated laterally (0), with shallow excavations (1), or deep excavations (2).
- 80. Distal end of scapular blade in lateral view: broad (0), or narrow (1).
- 81. Base of scapular blade: broad (0), or pinched (1).
- 82. Triceps process of posterior coracoid: small (0), or large and thumb-like (1).
- 83. Medial width of clavicular head: broad (0), or narrow (1).
- 84. Shape of anterior end of interclavicle: rhomboidal (0), or T-shaped (1).
- 85. Limb proportions: short and stout (0), or long and slender (1).
- 86. Entepicondyle of humerus: large (0), reduced (1), or greatly enlarged (2).
- 87. Ectepicondylar foramen of humerus: absent (0), or present (1).
- 88. Deltopectoral ridge of humerus: double (0), or single (1).
- 89. Dorsal groove of ilium: present (0), or absent (1).
- 90. Posterior process of ilium: slender and extends to or close to level of posterior limit of ischium (0), or short and does not reach posterior limit of ischium and possesses dorsal process (1).
- 91. Lateral pubic tubercle of pubis: present (0), or absent (1).
- 92. Proximal articulation of femur: narrow dorsoventrally (0), or broad dorsoventrally (1).
- 93. Ventral ridge system of femur: prominent (0), or feeble (1).
- 94. Proportions of calcaneum: width and length subequal (0), or length noticeably greater than width (1).
- 95. Lateral centrale of pes: present (0), or absent (1).



